THE ORIENTING OF AUDITORY ATTENTION: EVENT-RELATED POTENTIAL INVESTIGATIONS

Juliet Sara Holdstock

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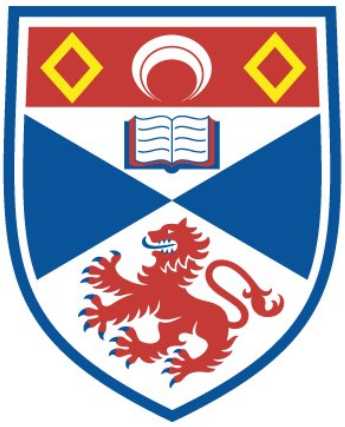

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Declaration for the Degree of Ph.D.

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ABSTRACT

The P300 complex has been dissociated into a parietally maximal P3b and a more anteriorly distributed P3a in auditory, visual and somatosensory modalities. The seven experiments reported in this thesis investigate the variables affecting the elicitation of the P3a. The Knight et al. (1989) paradigm was used which involves the presentation of frequent, rare target and rare nontarget auditory stimuli.

Experiment 1 showed that the P3a was elicited by novel sounds (environmental noises) when presented as rare nontargets in a sequence of frequent and target tones. When the rare nontarget novel sounds were presented in a sequence of other novel sounds the P3a was not elicited (Experiment 2). Experiment 3 showed that making the rare novel sound a target abolished the P3a, as did omitting the frequent stimuli from the sequence (Experiment 4). In the experiments in which the P3a was abolished, the novel sounds were found to elicit a P300 deflection with a parietally maximal scalp distribution (P3b). Other experiments showed no indication of habituation of the P3a over subsequent stimulus presentations (experiment 6) but did show that the amplitude of the P3a was larger when preceded by several stimuli different to the eliciting novel sound, than when immediately preceded by the identical sound (experiment 7). In contrast to novel sounds, tones did not elicit a P3a, even when presented as rare nontargets among frequent and target novel sounds (experiment 5).

The findings were related to a recent model of auditory attention (Naatanen, 1990). The P3a was interpreted as reflecting a process related to the orienting of attention resulting from the detection of a mismatch between present and previous stimuli.

CHAPTER 1

GENERAL INTRODUCTION

1.1 RECORDING AND INTERPRETING EVENT-RELATED POTENTIALS

1.11 RECORDING THE EVENT-RELATED POTENTIAL

An Event-Related-Potential (ERP) is an electrical field produced by the brain which can be recorded by electrodes attached to the surface of the scalp. The electrical field occurs at a fixed time with respect to the processing of a particular physical stimulus, the occurrence of a particular psychological process or in preparation for motor activity. In other words, it is a characteristic change in the electro-encephalogram (EEG) related to a particular brain process. The technical and methodological aspects of ERP recording are well explained by Cooper, Osselton and Shaw (1980) and Picton (1981), who provide information which is of particular relevance when using ERPs to investigate psychological processes. This section will therefore only provide a summary of the technique of ERP recording.

ERPs are recorded from the scalp by electrodes positioned according to a standard system of electrode placement (the ten-twenty system, Jasper, 1958). The number of sites used varies between studies depending on recording capacity of the equipment and the interests of the investigators. It is favourable to record from a large rather than a small number of sites because a larger number of electrodes allows a more complete description of the changes in the electrical potential field across the scalp.

An ERP waveform reflects the potential difference between two electrodes. Bipolar recording measures the potential difference between two electrodes on the scalp. Usually this method measures the potential difference between adjacent electrodes arranged in a chain across the scalp. A disadvantage of bipolar recording is that if a large potential is recorded synchronously at a number of electrodes which are being compared, it will be common to the recordings from these electrodes and so will be of small amplitude in the ERP waveforms which reflect the potential difference between the electrodes. More frequently a common reference derivation is used in which each channel records the potential difference between the recording electrode and a single common reference electrode. The reference may be placed so as to minimise the recording of potentials produced by the brain, for example, the right and left mastoids, the tip of the nose or a non-cephalic reference, for example, Stephenson and Gibbs (1951). It cannot be assumed that the reference electrode will pick up no brain activity and therefore cannot be considered to be neutral. The common reference method has the advantage that if a large potential is produced at several active electrodes it will appear with equal contribution in the waveforms recorded from each. When interpreting the ERP waveform, it is important to take into consideration the position of the reference electrode since position of the reference in relation to the potential field can have large effects on the apparent distribution of the EEG activity. If the reference is located so that it records the same potential field as the recording electrodes the potential difference between the two inputs to the recording channel will be small and little activity will be seen in the trace. If the reference is located at a distance from the potential field recorded by the recording electrodes, the potential difference will be large and a large amount of activity seen in the trace. A third recording derivation involves the use of an average reference. This technique involves averaging the activity recorded from the scalp electrodes and using this averaged activity as a common reference. This

means that for each recording channel, the potential difference is found between a single scalp electrode and the average activity over all the scalp electrodes. In practice the common reference method is employed most frequently.

An ERP consists of a series of positive and negative deflections whose configuration is characteristic of a particular stimulus or task. Due to its very small amplitude this response is hidden by the ongoing EEG activity and so is only observable after the signal to noise ratio (ERP=signal, EEG=noise) of the recording is improved. Signal to noise improvement is achieved by a method called "signal averaging".

Signal averaging involves repeating the task or presentation of the stimulus a number of times and for each trial recording the electrical activity over the period of interest. The recordings are then summed and divided by the number of presentations. In order to be dealt with by the averagers, the continuously varying waveform has to be reduced into a series of discrete numbers which is achieved by analogue to digital conversion. First, however, the signal is amplified so that it is large enough to be dealt with by the converters. The analogue to digital converter samples the EEG at a number of points in time starting just prior to the event and ending just after. The amplitude of the waveform at each sampling point is stored in the averager. Sampling begins prior to the event to provide a pre-stimulus baseline against which the amplitude of peaks in the ERP can be measured. The sampling rate determines which components of the ERP it is possible to resolve. The theoretical maximum resolution is half the sampling rate, so a sampling rate of 100 sampling points per second would not allow waves with a frequency of more than 50 Hz to be detected.

Averaging assumes that background electrical activity is random with respect to the event and so, on averaging, the mean value at each sampling point will be zero, i.e. the EEG will approach a straight line. "If the background activity is a normally distributed random variable, its amplitude range decreases by a square root factor of the number of trials averaged" (Picton, 1981). In contrast, it is assumed that the ERP is similar for each trial and so will remain constant during the averaging process. It is possible that the background EEG may not be completely eliminated which produces a problem in that the extent to which the background EEG is affecting the amplitude of the ERP is unknown. Summation may be used as an alternative to averaging because when a number of waveforms are added together the ERP continues to increase in size according to the number of trials being added, whereas the background activity will only increase by the square root of the number of trials thereby making the ERP more visible. Averaging, however, is the predominantly used method.

There are a number of points which should be kept in mind when interpreting averaged ERPs. One problem is that it is not known whether the final waveform represents the true ERP or whether it is just background EEG activity which has failed to be completely eliminated. This can be resolved by comparing the ERP trace with one obtained by alternately adding and subtracting the recordings so that the ERP effect is cancelled out, leaving only the background EEG activity (Schimmel, 1967). Another problem is that the average gives the mean amplitude and latency of the individual ERPs but gives little indication of the changes in ERP amplitude and latency over the trials. This means that the same averaged waveform could be obtained from a series of ERPs of similar amplitude or a series of variable amplitude ERPs. In a similar way, changes in latency of the peaks across trials could change the amplitude, latency and morphology of the resulting waveform

(Callaway, 1975). Since averaging relies on repeated recordings of the ERPs and assumes that the ERP occurs at the same time on each trial, the technique is unsuitable for investigating brain processes that occur only occasionally and those which occur at a variable latency with respect to the stimulus or event.

1.12 RECORDING ARTIFACTS

Electrical activity not generated by the brain may be recorded by scalp electrodes and produce an artifact in the trace. If this is synchronised with the stimulus it makes it particularly difficult to determine the morphology of the ERP produced by the brain.

Nonphysiological artifacts include those produced by the subject's movements which cause a change in electrostatic potentials produced by friction with clothing. These can be reduced by adequate grounding of the subject. Other artifacts include potentials induced by electromagnetic fields surrounding powerlines, electrical transformers and electrical motors. These are reduced by shielding the area with material of high electrical conductivity and magnetic permeability. Balanced or differential amplifiers are used to minimise contamination of the waveforms by nonphysiological artifacts. Signals which have the same effect on both the active electrode and the reference are not amplified (e.g. nonphysiological artifacts which affect all electrodes in the same way). In contrast, signals which have a differential effect on the active and reference electrodes are amplified.

One of the major physiological artifacts to affect recordings are eyeblinks. A standing potential of several millivolts exists between the cornea and the retina. On

blinking, a positive potential is produced in the anterior scalp by connecting these areas to the positive potential present at the cornea (Matsuo et al., 1975). Movement of the eyes, for example from side to side, also produces a positive potential in the areas of the scalp in the direction of eye movement (Hillyard and Galambos, 1970). Eye activity therefore contaminates ERP recordings from anterior electrode sites. One way to deal with this problem is to monitor the artifacts using peri-orbital electrodes and reject contaminated trials from averaging. The electro-oculogram can be averaged simultaneously to ensure that rejection is effective. Eyeblink correction procedures can also be used which estimate the average eyeblink from the ERP recordings and weight this according to the distance of the recording electrodes from the peri-orbital electrodes. The weighted average eyeblink is then subtracted from the ERP waveforms contaminated by eyeblinks (e.g. O'Toole and Iacono, 1987).

Small reflex responses may be produced by the scalp musculature particularly in response to stimuli which are very intense. These responses produce artifacts in the recordings and make interpretation of the portion of the waveform between 8-80ms after stimulus presentation very difficult. Large electrical fields are produced by movement of muscles in the face and the tongue which can be picked up by scalp electrodes and may therefore contaminate recordings. Finally, artifacts can be caused by potentials produced in the skin underneath the electrodes. These potentials can be reduced by lowering the interelectrode impedance as much as possible.

1.13 NEUROPHYSIOLOGICAL BASIS OF ERPS

The scalp recorded ERP reflects the potential difference between two recording electrodes which, due to their differing locations, are recording different combinations of potential fields produced by neurons in the brain.

The potential fields are produced by ionic current flow across cell membranes of active neurons which gives rise to a potential difference between different locations in extracellular space. This potential difference can be recorded by electrodes in contact with the extracellular space and the spatial distribution of such potentials gives rise to the potential field.

There are two types of transmembrane current flow. These are action potentials, which reflect transmission along the axon from the cell body to the axon terminals, and post-synaptic potentials which reflect information transmission from one neuron to another. Both types of transmission contribute to extracellular potential fields. ERPs were initially thought to result from the summation of action potentials (Adrian, 1941) and this has been found to be true for short latency ERP components elicited by somatosensory and auditory stimuli. Eccles (1951) and Elul (1972), however, have suggested that scalp and cortical surface ERPs mainly result from post synaptic potentials (PSPs). This proposal has support from a number of different types of evidence. For example, PSPs and surface ERPs often have similar waveshapes and durations (Humphrey, 1968b; Biedenbach and Stevens, 1969; Creutzfeldt et al., 1969). Anaesthesia, which blocks the generation of action potentials, has been found not to affect PSPs nor surface ERPs (Amassian et al., 1964). Finally Towe (1966) has used theoretical calculations to show that PSPs are sufficient to account for cortical surface ERPs in the cat somatosensory cortex.

During an action potential there is an outward flow of current from the neuron towards the approaching region of depolarisation; this produces a positivity in the adjacent region of extracellular space. During depolarisation there is inward current flow producing negativity in the adjacent extracellular space. Finally, as the depolarisation passes there is inward current flow and a positivity produced in the adjacent extracellular space. If an electrode is located adjacent to the neuron and another at some distance from it, the potential difference between the two electrodes will be recorded as positive, negative, positive as the depolarisation passes.

Turning to synaptic potentials, excitatory synapses produce inward current flow at the synapse which can be recorded as positive within the cell and negative in the extracellular space. The reverse is true for an inhibitory synapse.

The orientation of the cells and their configuration determines whether the potential field produced can be recorded at a distance from its generator. 'Open fields' are produced by parallel bipolar cells, such as Purkinje cells, which produce a dipolar field. If a group of these cells are oriented in the same direction it will be possible to record the potential field at a distance. If the cells are differently oriented the potential fields cancel each other and no extracellular potential field will be recorded. A second kind of field, the 'closed field', is produced by neurons which are multipolar with dendrites extending in many different directions from the cell body. In this situation the current flow is radially inwards which produces zero potential outside the nucleus so that no potential field can be recorded.

Scalp electrodes will therefore only record a fraction of the electrical activity produced by the brain at a specific time. It is possible to record 'open fields'

produced by groups of synchronously firing aligned neurons, e.g. the primary afferent volley from the thalamus to the cortex. However, if neuronal groups fire at different times with respect to the stimulus, if they have both excitatory and inhibitory effects or if the neurons are arranged in an unstructured way, the fields produced will not be recordable from the scalp.

When recordings are made close to the source of a potential field, the amplitude is large but small changes in electrode location have large effects on amplitude. In contrast, when recordings are made at a distance from the source (e.g. recordings from the cortical surface and scalp) the amplitude is small and even relatively large changes in electrode location will have little effect on the amplitude of the potential (e.g. Wood and Allison, 1981). The rate of change of the amplitude of an ERP component, across a number of electrode sites, can therefore provide information about the distance of the generator source from the recording electrodes. When the scalp electrodes are close to the source, the rate of change of the ERP component amplitude across the electrodes is fast.

In addition to the attenuation in amplitude and decrease in spatial resolution of the potential in moving from "near to far field" recordings, there is a further decrease in both when moving from intracranial to scalp recording. The magnitude of these further decreases depends on the depth and spatial extent of the source. The potential produced by focal superficial sources shows a large amplitude attenuation and decrease in spatial resolution; that produced by extensive deep sources shows little change from intracranial to surface recording. Duration also has an influence on potentials recorded from a distance because of its effects on temporal and spatial summation (Humphrey, 1968a,b), for example, there is a larger decrease in

amplitude from intracranial to scalp recorded potentials for short than for long duration potentials.

1.14 ERP SOURCE LOCALISATION

The location of the generator of an ERP component can not be directly inferred from the potential field recorded from the scalp. Two levels of localisation can be attempted. Using ERP data, localisation at a macroscopic level can be attempted in which potential fields recorded from the scalp are related to equivalent dipole sources in the head. At a more microscopic level, attempts have been made to determine the distribution of inward and outward transmembrane currents from the extracellular potential field.

Attempts at source localisation have employed volume conduction theory. Two approaches can be taken, one corresponds to the direct problem in which the surface potential field is calculated from a given source. The second corresponds to the inverse problem in which the source location and orientation is calculated from the surface potential field. It is not possible to solve the inverse problem because a scalp potential field may be explained equally well by an infinite number of proposed generators. The following approach is therefore adopted: first a source is assumed with a particular location and orientation, its surface potential field is calculated and compared with the empirical surface potential field. The location and orientation of the generator is then changed and the procedure repeated until a minimum difference exists between the calculated and empirical potential field (e.g. Wood and Allison, 1981; Scherg, 1989). Simplifying assumptions have to be made about the source; it is assumed that the surface recorded potential is produced by one or more point dipole sources which most fields approximate. Assumptions are also

made about the conducting medium, for example, in the dipole localisation method, Sidman et al. (1978), the head is treated as 3 concentric spheres all being homogeneous isotropic conducting media with resistivities of brain and scalp being equal but that of the skull being 80 times as great.

In order to constrain the number of possible neural generators for a particular scalp potential field, account is taken from a number of different types of evidence. This includes intracranial recordings in animals and humans, and surface recordings in animals and humans with known lesions. There are some problems with these types of recordings. Human intracranial recordings are performed on patients with brain dysfunction and so the results may not be generalisable to the population in general. In addition, the electrodes are located for therapeutic purposes and so may not be suitably placed for good assessment of cerebral ERP sources. Nonhuman studies are limited by the unknown extent to which animals are physiologically and psychologically similar to humans which produces the problem of the extent to which the findings of this research can be generalised to humans. This is a greater problem when considering ERP components whose occurrence is related to the psychological processes active during the task than when considering components generated by activity in the primary sensory systems which are phylogenetically old and so are likely to be similar across species. Interpretation of lesion studies is also problematic for both human and animal data. Firstly, the effect of a lesion may extend further than is apparent, for example, affecting fibre pathways or being diffuse and therefore affecting a large area with no clear boundary. Secondly, if an ERP can no longer be recorded following a lesion, a number of explanations exist other than that this area is the generator. For example, the lesion may have removed some facilitation which is usually necessary for the ERP to be generated or released an inhibitory process or distorted the conducting medium. All that can be concluded

is that the integrity of this area is necessary for the generation of the particular component. In addition, if a lesion has been the result of surgery or injury which has left a skull defect, the potentials over the entire scalp may be changed. Due to its lower conductance than the brain and scalp, the skull provides a barrier to the flow of current from the generator to the scalp. A skull defect, therefore. may provide a preferential path for current flow and so distort the potential field recorded from the scalp. This means the apparent effect of a lesion, on the ERP waveform, may actually be due to damage to the skull. More information is obtained if a lesion in a particular area does not affect the scalp ERP. Such a result indicates that the generator cannot be located in this area which puts a constraint on its possible location.

Each source which produces an electric potential field also produces a magnetic field. The magnetic field is at 90 degrees to the electric field and, if it is produced by a source which lies at least partially tangential to the surface of the head, it will be recorded by scalp electrodes. Comparison of ERP and MEG findings can aid in the evaluation of alternative hypotheses since postulated sources should be able to account for the potential fields of both.

A source determined by the dipole localisation method, which adequately accounts for an electrical potential field, does not necessarily correspond to the location of the true biological generator if multiple rather than single sources are involved (Wood, 1982). The dipoles identified are referred to as equivalent because "their field gives an equivalent description of compound activity of all neuronal elements in their vicinity which are oriented in parallel to the dipole axis" (Scherg, 1989). For ERP components which are thought to result from the activity of a single neuronal generator, identification of the equivalent dipole can assist in identifying its

biological generator. In the case of ERP components which are thought to result from the activity of diffuse or multiple generators, for example, P3b of the P300 complex to be discussed later, the location of the equivalent dipole may provide misleading information with regard to location of the biological generator. A potential field produced by a diffuse superficial source will be adequately modelled by an equivalent dipole at the centre of the active brain region and deeper in the brain.

1.15 ERP COMPONENTS

As mentioned earlier, the ERP consists of a series of positive and negative deflections. The recordings from the electrodes on the scalp are compared with those from a reference electrode located so as to be minimally affected by the potential field of interest. Depending on how these electrodes are connected to the recording apparatus, positive will be represented as an upward or downward deflection on the trace. The peaks of the ERP are labelled according to their polarity and either their latency after stimulus or task onset or the sequence in which they occur.

Although the peaks in the waveform are convenient to measure, they do not necessarily correspond to individual cerebral events. A positive deflection at one electrode and a negative deflection at another electrode may be reflecting the contribution to the ERP waveform of the same cerebral processes. The difference in polarity between the two electrodes would be caused by a phase reversal between the two caused by the location and orientation of the equivalent dipole. Similarly, a peak of the same latency and polarity at different electrode sites may be reflecting the activity of different generators. A major problem for the interpretation of the

ERP waveform is that a number of cerebral events may be contributing to the waveform at any point in time. One technique which attempts to identify independent contributions to the variance of the ERP is Principal Component Analysis (PCA) (e.g. K.C. Squires et al., 1977). PCA attempts to reduce the ERP waveform to a small number of factors and to estimate the relative contribution of these to the waveform. It is assumed that the factors correspond to the 'components' of the waveform. The effectiveness of the procedure is reduced, however, if there are changes in the latency of the component or nonlinear interactions among the different components. Donchin et al. (1978) define an ERP component as "a subsegment of the ERP whose activity represents a functionally distinct neuronal aggregate.....it is assumed that neuronal aggregates whose activity will be represented by an ERP component have been distinctly affected by one or more experimental variables." Naatanen and Picton (1987) suggest a more limited definition of an ERP component in that it refers back to localized physiological activity. These authors suggest that a component is "the contribution to the recorded waveform of a particular generator process such as the activation of a localized area of cerebral cortex by a specific pattern of input". In order to use ERPs to gain further information about cognitive processes, it is important to look at the variance in the waveform due to experimental manipulations even if the system affected is not anatomically distinct, rather than investigating contributions from localised physiological systems only. If the manipulations cause changes in a region of the waveform which are independent of what happens in the rest of the waveform, this region can be considered to be a component of the ERP. Attempts at locating the equivalent generator of a particular component, however, assume that the contribution to the waveform is produced by localised activity. The definition of an ERP component may differ therefore between researchers, depending on the aims of their investigation. Attempts to determine the structure of the ERP have identified

exogenous, endogenous and mesogenous components. These will be discussed in turn below.

Exogenous components usually occur within the first 100 ms or so after stimulus presentation and reflect early processing which is dependent on the physical characteristics of the stimulus. Examples of these include the auditory brain stem response (first described by Jewett and Williston, 1971) which consists of a series of six waves occurring during the first 10 ms after presentation of a sound. These waves are very insensitive to psychological variables and can even be recorded from comatose patients (Chiappa, 1983). Electrical stimulation of the median nerve at the wrist also produces an exogenous component, which has a latency of 20 ms and is maximal over the contralateral hand area of the sensorimotor cortex. Other exogenous components include visual ERPs elicited by the reversal of a black and white checkerboard. The latency and amplitude of the main ERP component produced (P100) is dependent almost entirely on the stimulus parameters such as the intensity of the stimulus.

Mesogenous components occur approximately 50-250 ms after stimulus presentation. These components are affected by both stimulus parameters and psychological factors. The N1 deflection, recorded from the vertex, consists of a number of mesogenous components. The amplitude of these components is sensitive to transient aspects of stimulation (Graham, 1979; Loveless, 1983; MacMillan, 1973). When the transient aspects are controlled similar N1 responses are elicited by different kinds of acoustic stimuli, e.g. clicks, tones, speech, animal sounds (Naatanen and Picton, 1987). These components, however, are also susceptible to modulations of the general state of the individual. These modulations include changes in arousal due to changes associated with the sleep-wakefulness

cycle, drugs and alcohol, circadian rhythms and involvement in the task; whether the presented stimuli are relevant or irrelevant to the task and the temporal uncertainty of the next significant stimulus. The N100 complex will be discussed in more detail in section 1.27 of the present chapter.

The investigation of endogenous components has been important in psychology. The occurrence of these components is related to the psychological processes active during the task. The investigation of endogenous ERP components therefore supplements knowledge obtained from traditional cognitive psychology by providing a real time correlate of psychological processes. Endogenous ERP components are particularly important for providing information about the timing of psychological processes which are not open to introspection (e.g. preconscious processes) or behavioural observation. A number of different endogenous components have been identified which will be briefly described below.

The most widely investigated group of endogenous ERP components is the P300 complex. This consists of an N2 component, which has a modality specific scalp distribution and may reflect recognition of an informative target within a specific sensory channel (Simson, Vaughan and Ritter, 1976, 1977a); a P3a wave with a frontocentral distribution, occurring in response to improbable stimuli whether or not they are task relevant; a P3b wave, with a centroparietal distribution, occurring in response to task relevant stimuli and a centroparietally distributed slow wave. This complex of components is the subject of the experiments reported in this thesis and so will be discussed in more detail in section 1.2 of the present chapter.

A slow negative shift occurs before self-initiated movement when no external stimulus is present, this has been termed the readiness potential (Deecke et al., 1969;

Vaughan et al., 1968; Gerbrandt et al., 1973; Kutas and Donchin, 1974). The negativity starts several hundred milliseconds before the movement and shows a widespread scalp distribution with some localisation over the cortical areas controlling the appropriate muscles. Following movement there is a complex series of waves reflecting sensory feedback from the movement.

Another endogenous component is the contingent negative variation or CNV (Walter et al., 1964). This is a negative baseline shift which develops between a warning stimulus and an 'imperative' stimulus requiring a response. An early negative peak occurs shortly after the warning stimulus (the 'O' wave) and is followed by a negative wave which occurs before the imperative stimulus (the 'terminal' wave). The 'O' wave is thought to reflect a general response to significant or novel stimuli and can be elicited in CNV and non-CNV tasks. The 'terminal' wave is thought to be related to motor response processes and to correspond to the readiness potential (Rohrbaugh and Gaillard, 1983).

1.2 GENERAL INTRODUCTION TO THE P300 COMPLEX

The endogenous ERP component to receive the most research interest has been the P300. This has been for a number of reasons, which include the large amplitude of the deflection and its consistent elicitation in a number of tasks. The potential diagnostic value of the P300 has been suggested by reports of changes in its latency with mental dysfunction, for example, retardation (Squires et al., 1979) and dementia (Brown et al., 1982; Pfefferbaum et al., 1984; Polich et al., 1986), and changes in amplitude in disorders such as schizophrenia (Barrett et al., 1986). This has stimulated further research into the psychological significance of the P300.

Sutton published the first report of a P300 in 1965. The study described a positive going deflection with a latency of approximately 300 ms in response to auditory (click) and visual (light flash) stimuli whose occurrence, after a cue stimulus, was uncertain. Sutton reported that the amplitude of the P300 was larger in response to stimuli which had a low probability of occurring after the cue, compared with high probability stimuli. Since this initial report, positive deflections with latencies of 300-600 ms have also been reported in the somatosensory modality and in experimental paradigms other than that used by Sutton. These positive deflections have all been termed P300. Recent research, however, suggests that the P300 is not actually a unitary phenomenon but that it can be dissociated into at least two positive components, termed P3a and P3b, which are thought to be indicators of different psychological processes (see section 1.22). Although a large literature now exists describing the eliciting conditions of the P3b component, there has been no systematic study of the variables affecting the elicitation of the P3a. The conditions necessary for the occurrence of the P3a were therefore investigated in the series of experiments reported here. The initial experiment in this thesis (Chapter 4) was conducted in order to confirm the previously reported dissociation of the auditory P300 complex into P3a and P3b components. Subsequent experiments investigated the variables affecting the elicitation of the P3a, thus providing information necessary for uncovering its psychological significance.

This introductory review attempts to provide the reader with a brief, general background of P300 research. The experiments reported in this thesis are concerned mainly with the P3a and therefore only a brief review of the P3b literature will be given. The discussion of findings which are of particular relevance for a specific experiment will be postponed to the Introduction of the relevant chapter. The

review will be divided into several sections. I will start by describing various versions of the oddball task which is the paradigm most widely used in P300 research. I will then discuss research reporting the dissociation of the P300 complex, briefly review the literature on the P3b, including the results of studies prior to the dissociation of the P300 complex (which were concerned with what is now considered to be the P3b), and review the main theories of the functional significance of the P3b. Finally, I will describe Naatanen's theory of automatic and controlled processing of auditory stimuli which is used as a framework within which to interpret the P3a results obtained in the present experiments.

1.21 ODDBALL TASKS

The most frequently used paradigm in P300 research has been the oddball task. In its most basic form the oddball task is a go/nogo task in which two stimuli are presented with different a priori probabilities, e.g. frequent stimuli with a probability of 0.70 and targets with a probability of 0.30. The design of the oddball task is particularly suited to ERP research because a number of trials of each condition are presented which allows the responses to stimuli in each condition to be averaged. Averaging of a number of responses is necessary to eliminate background noise activity from the ERP waveform (see section 1.11). The task also allows several different variables to be manipulated easily. These variables include stimulus probability, whether a response is required and direction of attention. The extent to which the stimuli in the sequence differ can be manipulated, for example, the stimuli may be tones of different frequencies or different intensities or stimuli of different categories such as tones and other sounds. The same paradigm can also be used in different modalities allowing comparisons between modalities to be made.

As the studies reported here are concerned with ERP responses to auditory stimuli, I will give examples of various versions of auditory oddball tasks. Equivalent tasks have been used in the visual and somatosensory modalities.

In a two stimulus oddball task, the subject is presented with a sequence of stimuli consisting of, for example, a tone with a high probability of occurrence randomly mixed with a low probability tone of a different frequency or different intensity to the high probability stimulus. The task assigned to the subject is to make a response (specified by the experimenter) whenever the low probability tone occurs. The responses are usually incrementing a mental count of the number of target stimuli so far presented or pressing a button to indicate that a target has been detected.

The three stimulus oddball task is a variation of the task described above. The subject is presented with a stimulus sequence consisting of randomly mixed high probability stimuli (frequent, e.g.0.70) and two other stimuli (or categories of stimuli) with equally low probability (e.g. 0.15). The subjects are instructed to respond to one of the low probability stimuli (target) and are either instructed not to make any response to the other low probability stimulus or are not told that it will be presented (rare nontarget). The stimuli assigned to the three conditions (frequent, target, rare nontarget) can be varied. The three stimulus oddball task used in the first experiment reported here presented a high tone as the frequent, a low tone as the target and segments of environmental noises as the rare nontargets.

Both types of oddball task described above would be considered by Naatanen to be 'one channel' attentional tasks because the subjects have to attend to all the stimuli in order to detect the deviant stimulus. According to Naatanen (1990), the rare

stimuli would not occur frequently enough for an attentional trace of their features to be maintained, so they could not be selectively attended to in order to detect the target (this is discussed in more detail in section 1.28 of this chapter). Other variations in design of the experiments using oddball tasks have been concerned with whether the subject is attending to the stimulus sequence.

In passive oddball paradigms (Sams et al., 1985) the subject is engaged in another task (e.g. reading) whilst the stimulus sequence is presented. No responses are required to the presented stimuli. It is usually assumed that the stimulus sequence has been ignored but it is possible that tasks such as reading do not focus attention strongly enough, making it possible for the subject to shift attention to the sequence of sounds throughout the task.

Dual task studies have required the subject to perform a task (e.g. perceptuo-motor) whilst detecting targets in a two stimulus oddball task. These tasks have been used to look at the extent to which the components of the ERP elicited by the targets in the oddball task are dependent on the amount of processing resources available at a particular time (see Kramer and Spinks, 1991).

Two channel oddball studies are versions of dichotic listening studies. Subjects are presented with a different sequence of stimuli to each ear. Each sequence consists of a frequent and rare stimulus. The subject is told to respond to the rare stimuli from the sequence presented to one ear only. This paradigm allows the investigation of the effects of attention on the processing of the stimuli in each sequence.

One should be cautious in referring to attentional channels. It is possible that stimuli are selected for attention according to the features which are easiest to discriminate.

In dichotic listening studies, for example, it is usually easier to discriminate between the ears to which the stimuli are presented than between the frequencies of the stimuli. Subjects therefore attend to a particular ear (attentional channel) and then discriminate the frequency to respond to. If the difficulty of location discrimination is increased, subjects may first attend to the frequency of the stimuli and then discriminate the ear of presentation in order to detect the target. In this case frequency is the attended channel.

The two and three stimulus oddball tasks and the attended channel of the dichotic listening task are all examples of active oddball tasks. According to Naatanen (1991), the main interest in active oddball tasks is in the brain processes associated with "purposeful discrimination" of deviant stimuli among standard stimuli. The ignored channel of the dichotic listening task is an example of a passive oddball task which is used to "study brain responses to ignored stimuli and those underlying involuntary discrimination of, and attentional switches to deviant stimuli among ignored stimuli" Naatanen (1991).

The P300 complex has also been elicited by stimuli in a number of paradigms other than the oddball task. These include feedback tasks, signal detection tasks, matching tasks and language tasks. Pritchard (1981) provides a very good review of the effects of manipulations, within these paradigms, on the P300 complex.

1.22 DISSOCIATION OF THE P300 COMPLEX

At least two dissociable positive components of the P300 complex have been identified in the visual, auditory and somatosensory modalities. These components

are a P3a, which has a fronto-central maximum and peak latency of 270-350 ms, and a later P3b, with a more posterior distribution and peak latency of 300-600 ms. Other components considered to be part of the P300 complex include a negative component (N2) preceding the P3a and a positive slow wave with a centro-parietal maximum and a latency of 500-1000 ms. The research reviewed here concerns the dissociation of the P3a and P3b components.

Considering first the visual modality, Courchesne et al. (1975) recorded visual event related potentials elicited by stimuli presented rarely and randomly within a sequence of background stimuli (the number 2). The rare stimuli included the number 4 which had to be counted and two types of intrusive stimuli (simple, easily recognisable figures and complex unrecognisable figures) which did not require a response. Both the simple figures and the counted stimuli elicited a P300 with a latency of 380-430 ms which was distributed maximally over posterior scalp sites. The unrecognisable complex stimuli elicited a large frontally distributed P300 with a latency of 360-380 ms.

Turning now to studies of the dissociation of the auditory P300, Squires et al. (1975) presented subjects with a sequence of tones in which there was an occasional change in intensity or frequency. In different blocks of trials the subjects were instructed to count the frequent stimuli, count the rare stimuli or ignore the stimuli and read a book. It was reported that attended rare intensity and frequency changes, whether or not they were being counted, elicited a parietally maximal P300 with a mean latency of 350 ms (this was labelled the P3b). This peak had a maximum amplitude at parietal sites. In the condition in which the subjects ignored the sequence of stimuli and read a book, a P300 with a latency earlier than that of the P3b was elicited by the intensity and frequency changes (this was labelled the P3a). The P3a was of

maximal amplitude at frontal and vertex sites. No P3b was elicited by ignored stimuli. In the attend conditions the P3b was preceded by a positive peak suggested by Squires et al. to be the same as the P3a elicited by rare ignored stimuli. It is not certain whether the P300 components described by Squires et al. (1975) correspond to those reported by Courchesne et al. (1975) since Squires et al. report a fronto-centrally distributed P3a in response to rare simple ignored stimuli, whereas Courchesne et al. report a frontally distributed P300 in response to attended rare complex unrecognisable stimuli. In the study of Courchesne et al. (1975), however, ERPs were not recorded in response to the visual stimuli whilst the subject was engaged in another task. It is therefore possible that if an ignore condition had been employed a P3a component similar to that reported by Squires et al. (1975) may have been produced in response to the rare stimuli. While subjects attended to stimuli in the study of Courchesne et al. (1975) the simple recognisable rare stimuli and the rare target stimuli elicited a posteriorly distributed P3b component, whereas the complex unrecognisable rare stimuli produced a P3a component. In the Squires et al. (1975) study the rare stimulus was neither complex nor unrecognisable, making it equivalent to the simple recognisable stimuli in the study of Courchesne et al. (1975). Consistent with the Courchesne et al. (1975) study, the rare auditory stimuli produced a posteriorly maximal P300 when attended. This therefore suggests that the studies of Courchesne et al. (1975) and Squires et al. (1975) are reporting similar phenomena. It should be remembered, however, that Squires et al. (1975) and Courchesne et al. (1975) were investigating the P300 elicited by stimuli in different modalities and, as the evidence concerning the modality nonspecificity of the P300 complex is equivocal, this may contribute to the differences found between the experiments.

In the studies of Knight (1984) and Knight et al. (1989), subjects were presented with sequences of auditory stimuli consisting of the random mixing of a frequent tone, a rare target tone and either one or several rare novel stimuli (short segments of environmental and computer generated sounds). The results of patients with discrete lesions are described below. The healthy control subjects showed a parietally distributed P300 (P3b) in response to the detected targets and a slightly earlier fronto-centrally distributed P300 (P3a) in response to the unexpected novel sounds. This appears to be consistent with the findings of Courchesne et al. (1975) in the visual modality.

Dissociation of the P300 complex in the somatosensory modality was reported by Yamaguchi and Knight (1991a). Subjects had to press a button in response to taps to the fifth finger occurring occasionally within a sequence of taps to the second finger. Two other types of infrequent stimuli which did not require a response were also presented, these were taps to the third or fourth finger and an electric shock to the wrist. Detected targets elicited a parietally maximal P300 (P3b) whereas both tactile and shock novel stimuli produced a P300 with a central maximum and earlier latency than the P3b (P3a). This result is therefore similar to the dissociation reported in other modalities.

The studies discussed above, reporting the dissociation of the P300 complex into P3a and P3b components, rely on the differences in latency and scalp distribution between the P3a and P3b in order to argue that these deflections are separate ERP components. Further evidence in support of a dissociation is provided by the results of studies of patients with lesions in specific cortical regions. The differing scalp distributions of the P3a and P3b components suggest that they may be reflecting the

activity of at least partially independent generators in the brain. Lesions would therefore be expected to have differential effects on the P3a and P3b components.

In the study described briefly above, Knight (1984) presented subjects with a sequence of tones among which two types of occasionally occurring stimuli were randomly interposed. The rare stimuli were target tones which required a button press response and an unexpected 'novel' sound which did not require a response. As discussed above, healthy control subjects produced a parietally distributed P300 in response to the target tones (P3b) and a fronto-centrally distributed P300, of slightly earlier latency than the P3b, in response to the novel sound (P3a). Subjects with unilateral prefrontal damage (maximal in the dorsolateral frontal cortex) produced a P300 in response to the target tones which did not differ from that elicited in the controls. In contrast, the P300 elicited in response to the novel sounds and the enhanced N200 preceding it,obtained in the waveforms of the controls, were not obtained in the waveforms produced by the prefrontally damaged patients. The patients produced a parietally distributed P300 in response to the novel sounds which, although earlier in latency, did not differ in amplitude or distribution from that elicited by the targets. Knight (1984) therefore suggested that the results of this study indicated that the prefrontal region was necessary in order to respond differentially to novel stimuli. The finding that the P3b was unaffected but the P3a abolished by prefrontal damage suggested that the integrity of this cortical region was unnecessary for the process generating the P3b but was necessary for that generating the P3a.

Knight et al. (1989) recorded auditory event-related potentials in response to occasional target tones and unexpected 'novel' sounds randomly presented within a sequence of frequently occurring tones. As in the study of Knight (1984) control

subjects elicited a P3b in response to the target tones and a P3a in response to the 'novel' sounds. Lateral parietal cortex lesions had no effect on either the P3a or the P3b. However, unilateral lesions of the temporal-parietal junction caused bilateral abolition of the P3a and P3b at parietal sites but partially preserved the P3a at frontal sites.

Yamaguchi and Knight (1991b) recorded somatosensory event-related potentials in response to mechanical taps to the fifth finger requiring a button press response, which were randomly interposed in a sequence of taps to the second finger. Two types of infrequent stimuli which did not require a response were also presented within the sequence; these were mechanical taps to the third or fourth finger and an electric shock to the wrist. In healthy subjects target stimuli had been found to elicit a P3b and both the mechanical and tactile novel stimuli had been found to elicit a P3a (Yamaguchi and Knight, 1991a). Temporal-parietal lesions were found to reduce the P300 elicited by all stimuli at all electrode sites with a maximum decrease in amplitude at parietal sites. Frontal lesions were found to reduce the P300 elicited by novel stimuli over frontal sites but not to affect the P3b elicited by target stimuli. Patients with parietal lesions produced normal P300s in response to all stimuli except for contralateral shock novel stimuli which produced a reduced amplitude P300.

The results of these studies therefore support the dissociation of the P300 complex into P3a and P3b components which appear to be produced by the activity of at least partially separate physiological systems. For both the auditory and somatosensory modalities the integrity of the temporal-parietal region appears to be necessary for the generation of the P3b component in response to target stimuli; in addition, the

prefrontal region needs to be intact for the generation of the P3a component in response to unexpected novel stimuli.

To summarise, the results of experimental studies on healthy subjects and studies investigating the effects of discrete brain lesions suggest that the P3a and P3b are separate components, elicited under different experimental conditions, which require the integrity of different areas of the brain for their production.

1.23 VARIABLES AFFECTING P3B

The P3b is elicited by detected target stimuli but this component does not occur if the identical stimuli are unattended (e.g. Squires et al., 1975). The P3b is produced in response to both target stimuli requiring a motor response and those requiring increment of a count, thus suggesting that the P3b is not related to the motor aspects of a task. Attended rare non-target stimuli have also been found to elicit a posteriorly distributed P3b-like component (e.g. Courchesne et al., 1975, 1978; Duncan-Johnson and Donchin, 1977), as have omissions of expected stimuli (Ruchkin et al., 1975). This suggests that the stimuli eliciting the P3b are not restricted to those which have been explicitly designated as targets by the experimenter.

The variables affecting the amplitude of the P3b are summarised in Johnson's triarchic model of P300 amplitude (1986, 1988). The model proposes that the amplitude of the P300 is determined by 3 dimensions (i) subjective probability, which can be further subdivided into the effects of a priori probability and expectancies produced by the structure of the stimulus sequence (ii) stimulus meaning, a general term which he uses for the effects of task complexity, stimulus

complexity and 'stimulus value' and (iii) information transmission. Johnson proposes that subjective probability and stimulus meaning have independent additive contributions to the amplitude of the P3b, whereas the amplitude determined by subjective probability and stimulus meaning is modulated in a multiplicative way by the amount of information transmitted about the stimulus. I will use Johnson's model as a framework to summarise briefly some of the studies investigating the effects of experimental manipulations on the P3b.

Subjective probability

Both a priori probability and expectancies formed by the subject contribute to P300 amplitude. An inverse relation has been found between a priori probability and P300 amplitude in a number of different tasks including counting (e.g. R. Johnson and Donchin, 1980; R. Jr. Johnson and Donchin, 1982) and reaction time tasks (e.g. Duncan-Johnson and Donchin, 1982, Johnson and Kopell, 1980), prediction tasks (Friedman et al., 1973) and 'feedback' tasks (Campbell et al., 1979). In prediction and feedback tasks, interest is directed to the stimulus which signals the correctness of the subject's response. The study reported by Friedman et al., (1973) involved subjects guessing which of several stimuli would be presented on the next trial, presentation of the stimulus providing feedback concerning the guess. Campbell et al. (1979) used signal detection and time estimation tasks where information about performance was provided throughout the task. The relation between a priori probability and P300 amplitude has been found for all types of stimuli including the omission of expected stimuli (Ruchkin et al., 1975). Experiments using a number of different stimuli as targets have found that the probability of the category of stimuli rather than the probability of individual stimuli is the determinant of P300 amplitude (e.g. Courchesne et al., 1977; Johnson and Donchin, 1980; Johnson et al., 1985).

In addition to the a priori probability of the stimuli in a sequence, the local structure of the stimulus sequence and the temporal probability of the stimuli affect expectancies of the occurrence of a stimulus. Sequential and temporal probabilities are important sources of information which combine with other things, such as the information given to the subject about the stimuli, to produce the subjective probability of the stimulus. In contrast with a priori probability, which is the true likelihood of a particular stimulus occurring, subjective probability can be thought of as the likelihood of a particular stimulus occurring calculated by the subject throughout the sequence.

Expectancies formed by the subject due to the sequential structure of the sequence have been found to affect P3b amplitude. K.C. Squires et al. (1976) were the first to quantify the relation between P300 amplitude and sequential structure. Stimuli which were repeated were found to elicit a smaller P3b than those which were not repeated. This study also investigated more complicated sequence effects. The effect of stimulus sequence on the amplitude of the P3b has been replicated in a number of studies (e.g. Squires et al., 1977b; Johnson and Donchin, 1980,1982). In the study of Johnson and Donchin (1980), one condition required one of three equiprobable tones in a sequence to be counted, whereas in a second condition, one of two tones with probabilities of 0.33 and 0.67 had to be counted. The P300s elicited by two uncounted stimuli were identical to that elicited by one uncounted stimulus which was twice as probable. The results suggested that the amplitude of the P3b was determined by the subjective probability of the target event and was associated with the category to which the stimulus was assigned rather than the physical stimuli. In the study of Johnson and Donchin (1982) subjects were presented with a sequence of two auditory stimuli each of which occurred with a

probability of 0.5 over the entire stimulus block. Throughout the stimulus block the probability of the two stimuli was changed, so for one segment of the sequence one stimulus had a probability of 0.33 and the other a probability of 0.67, whereas for another segment these probabilities were reversed. In one condition the subjects were unaware of these changes in probability whereas in a second condition subjects were informed of the changes. Amplitude of the P300 did not differ between the two conditions. This result suggested that the mechanism generating expectancies is largely automatic. Knowledge of the stimulus sequence was found to affect ERP responses at certain points in the sequence. Different effects on P300 amplitude were found in the two conditions at the points in the sequence where there was a transition between probabilities.

A problem exists in the interpretation of studies investigating sequential structure and probability as they have confounded the sequential probability with the temporal probability of the stimulus. Studies attempting to dissociate the effects of these two probabilities have found that temporal probability appears to be the determinant of P300 amplitude. The effects of stimulus sequence and temporal probability will be discussed more fully in chapter 10.

From the results of a feedback task, Tueting et al. (1971) suggested that 'outcome probability' is the determinant of P3b amplitude. Outcome probability was defined as the joint probabilities of guessing and stimulus (feedback) frequencies. It was found that a larger P300 was elicited when the subjects guessed that an infrequent stimulus would occur and were correct or guessed that a frequent stimulus would occur and were incorrect. Outcome probability appears to be similar to subjective probability.

Donchin and fellow researchers (K.C. Squires et al., 1976) have suggested that P300 amplitude correlates with surprise. They proposed that task relevant stimuli which were unexpected (surprising) elicited a P300. Donchin's group proposed a model of expectancy. The model proposed that expectancy was determined by the linear addition of (a) the memory of the frequency of the event within the prior sequence, (b) the structure of the stimulus sequence, i.e. the number of repetitions of stimuli of one class preceding the presentation of another stimulus and (c) the a priori probability of the stimulus. Expectancy of K. C. Squires et al. therefore appears to be very similar to the variable termed subjective probability by other researchers. However, not all surprising task relevant events elicit P300. Kutas and Hillyard (1980) showed that whereas physically anomalous terminal words of a sentence elicited a larger P3b than words which were not anomalous, semantically anomalous words elicited an 'N400' instead of an enhanced P3b. It was suggested that expectancies would be built up whilst reading the sentence which would be violated when the semantically anomalous terminal word was presented. This study suggests that expectancy or subjective probability can not be the only factor determining the elicitation of the P3b. Donchin's contemporary ideas concerning the P300 complex will be discussed in section 1.25.

Stimulus meaning

The amplitude of the P3b elicited by a particular stimulus varies depending on the subject's task. A number of studies have reported that a larger amplitude P3b is elicited by stimuli when the task is more complicated. Prediction of a stimulus (Chesney and Donchin, 1979), feedback time estimation (Johnson and Donchin, 1978) and paired associate learning (Horst et al., 1980) produced P3bs of larger amplitude than those elicited when the same stimuli were counted.

The complexity of the stimulus, independent of the task, has also been found to affect P3b amplitude. Verbaten (1983) found that when patterned visual stimuli were used, stimuli with a more intricate pattern elicited a P3b of larger amplitude.

A number of studies have reported the effects of stimulus value on the amplitude of the P3b. As seen above, the paradigms used in P3b research often involve classifying stimuli as either targets or non-targets. It has been found that with equiprobable stimuli, P3bs of slightly larger amplitude are elicited when the stimuli are targets compared with when they are non-targets (Duncan-Johnson and Donchin, 1977; Smith et al., 1970). Omission of a stimulus has been found to cause the release of a P300 only when the stimulus omission provides information (e.g. Klinke et al., 1968; Picton and Hillyard, 1974; Ruchkin and Sutton, 1973). A number of experiments have investigated the effects of monetary reward on the amplitude of P3b. For example, Sutton et al. (1978) presented subjects with two stimuli (S1 and S2) each of which could be a high or low tone. In order to win money the subject had to guess either both stimuli correctly or both incorrectly. The first stimulus was found to elicit a P300 which did not differ in amplitude whether the guess was correct or incorrect. The P300 following the second stimulus, which was the stimulus providing value information, was larger in amplitude than that following the first. The results, therefore, suggested that the value of the stimuli had a greater effect on P300 amplitude than feedback about the guess.

Information transmission

The final dimension which Johnson proposes as a determinant of P300 amplitude is information transmission. This is further subdivided into the effects of equivocation and attention.

Ruchkin and Sutton (1978a, 1978c) proposed that the amplitude of the P300 could be attenuated by equivocation which was defined as information loss due to a posteriori uncertainty. In P300 research, equivocation would refer to the uncertainty about having correctly perceived the event. This is illustrated by the finding that the P300 released on the omission of an expected stimulus is of smaller amplitude than that elicited by presentation of a stimulus. Ruchkin and Sutton (1978a) asked subjects to predict before each trial whether a stimulus would be presented. A different interval was used between the warning stimulus and target stimulus (700 ms or 1500 ms) in different blocks of trials. Latency corrected ERP averages were computed using a Woody procedure. The amplitude of the P300 elicited when the stimulus was omitted was smaller than that elicited by the presentation of the stimulus. This difference in P300 amplitude was larger for the longer interval between the warning stimulus and the time of stimulus presentation. Ruchkin and Sutton interpreted this finding in terms of the increased temporal uncertainty associated with perception of stimulus nonoccurrence at the longer interval (time estimation judgements at longer time intervals were found to be more variable thus supporting this interpretation). Also see Ruchkin and Sutton (1978b).

Elicitation of the P3b is highly dependent on whether the subjects are attending to the stimuli. In a discrimination task such as the oddball paradigm, according to Naatanen (1990) both the targets and non-targets are relevant to the task and would

elicit a P300 whose amplitude is dependent on the probability of the stimuli. When the stimuli are ignored, and are therefore irrelevant to the task, neither the targets nor the non-targets elicit a P3b (e.g. Desmedt and Debecker, 1979).

The results of dual task studies suggest that P300 is indexing some kind of limited capacity processing of the attended stimuli. The amplitude of the P300 is reduced when the subject is simultaneously engaged in two tasks compared with when the subject is only engaged in the P300 eliciting task. Towle et al. (1980) had subjects watch a travelogue tape about which they would later be tested, whilst simultaneously counting infrequent target tones. The amplitude of the P300 elicited by the target tones was smaller in the dual task condition than in a condition in which only the tones were being counted. Counting accuracy was also lower in the dual task condition. Isreal et al. (1980) report a series of experiments in which the subject was engaged in one of two primary tasks. The task was either perceptual (monitoring the movements of numbers of targets on a television screen) or perceptual motor (a tracking task). The secondary task was a choice RT task to one of two tones of different frequencies. When the subject was required to perform either of the primary tasks the amplitude of the P300 elicited in the choice reaction time task decreased in amplitude and reaction time increased. Increasing primary task difficulty from the perceptual to the perceptual-motor task decreased P300 amplitude and increased reaction time further. Making the tracking task more difficult, however, did not further decrease P300 amplitude. Pritchard concludes that these studies suggest that the P3b is related to a limited capacity of perceptual resources. This is supported by a study of Warren and Marsh (1979) who reported that there was no difference in P3b amplitude elicited by congruous and incongruous colour-word pairs in a Stroop task. The Stroop interference effect is thought to be due to response competition rather than competition for perceptual processing

resources and so would not have been expected to have any effect on the amplitude of the P3b.

The relation between P3b and resolution of a non-specific state

An area of discussion in P3b research has been whether the component is reflecting a specific process or simply a change from one level of alertness to another. Karlin (1970) suggested that P3b reflected resolution of a non-specific arousal state produced by the anticipation of signals. The contingent negative variation (CNV), a negative potential which builds slowly between a warning stimulus and a target stimulus in a warned reaction time (RT) task, shows a rapid return to baseline on presentation of the target stimulus. Wilkinson and Lee (1972) suggested that the P300, elicited in a task involving the increment of a mental count on the presentation of one of three equiprobable tones, "may perhaps be taken to indicate predominantly the magnitude of contingent negative variation return to baseline". In the study of Wilkinson and Lee, however, a discrete P3b was not elicited but a longer duration positive slow wave obtained in the waveforms of most subjects. These authors suggest that in other studies the positivity at approximately 300 ms may reflect contributions of both return to baseline of a CNV and discrete P3b activity. A number of studies have demonstrated the independence of the P300 and the CNV (e.g. Courchesne et al., 1975; Desmedt and Debecker, 1979). Desmedt and Debecker (1979) presented random sequences of equiprobable acoustic clicks and electrical stimuli to the index finger at random intervals. Subjects were required to count either the clicks or the electrical stimuli. The stimuli were of low intensity which made the task difficult. No CNV was obtained (the time constant used would have allowed a CNV to be visible in the waveform if present) but a centro-parietally maximal positive deflection with a latency of approximately 350 ms (P350) was

obtained. Desmedt and Debecker therefore suggested that the CNV and P350 were dissociable. The theory of the functional significance of the P3b proposed by Verleger (1988) appears to be suggesting that the P3b reflects the resolution of an anticipatory state. Verleger's theory will be discussed in detail in section 1.25. Briefly, the main proposal is that the P3b is elicited on the presentation of an awaited event in a highly structured task. It is suggested that the P3b reflects the release of "excess activity" from perceptual control areas which builds up while the subject is expecting the stimulus, thus allowing the stimulus to be processed. Pritchard (1981), however, has suggested that as P300 amplitude and latency have been found to correlate with a number of specific experimental variables, resolution of a non-specific state appears an unlikely explanation of the P300.

1.24 P3B LATENCY

Studies such as Ragot and Renault (1985) have reported a relation between reaction time and P3b latency. These authors reported that in a task which manipulated the compatibility between the spatial position of the stimulus and that of the response, incompatibility increased both reaction time and P3b latency.

A number of studies, however, suggest that the latency of the P3b depends on the time required for the completion of "stimulus evaluation" (Donchin, 1979) but that it is largely independent of response selection and execution time. McCarthy and Donchin (1981) presented subjects with either the word "RIGHT" or "LEFT" on a particular trial which was preceded by a warning stimulus ("SAME" or "DIFFERENT") indicating whether a response should be made with the same or opposite hand to that indicated by the target word. When subjects had to respond

with the opposite hand to that indicated by the stimulus, reaction time was increased to a larger extent than P3b latency. The manipulation affecting response selection was therefore found to affect reaction time but not P3b latency. Kutas et al. (1977) presented subjects with a task in which they were required to detect the occurrence of an infrequent stimulus presented among frequent stimuli where, in one condition, the stimuli were a female name and a male name and, in another condition, several female names and several male names. When the latency of the single trials was investigated, it was found that when the subjects were instructed to respond as fast as possible (i.e. reaction time was determined by response selection) the correlation between P3b latency and reaction time was low. When subjects were instructed to avoid making errors, the correlation between P3b latency and reaction time was much higher. In the latter condition reaction time was determined largely by stimulus evaluation. Coles et al. (1985) required subjects to make a motor response with one hand if one stimulus (the letter 'S') was present and to respond with the opposite hand if a different letter ('H') was present. The target letter was presented in the centre of an array surrounded by either the same letter (compatible noise) or letters which would require the opposite response (incompatible noise). Incompatible noise increased both reaction time and P3b latency. A warning tone was presented, prior to presentation of the array, on half the trials. The warning tone was found to shorten reaction time but had no effect on P3b latency. A final study of relevance here is that of Ford et al. (1982). These authors used the Sternberg task in which a response was required indicating whether a probe stimulus was or was not a member of the memory set (which consisted of either 2 or 4 digits). On half the trials the probe stimuli were degraded. Reaction time was delayed in both young and elderly subjects for larger memory sets, degraded probe stimuli and negative responses (indicating that the stimulus was not in the memory set). For the young subjects P3b latency was increased in response to the same variables affecting

reaction time. The elderly subjects showed an increase in P3b latency only in response to degraded stimuli. A differential effect of experimental manipulations was therefore found on reaction time and P3b latency in elderly subjects.

The studies suggest that completion of stimulus evaluation appears to be necessary before the occurrence of the processing reflected by the P3b but this does not imply that the P3b is a scalp recorded reflection of stimulus evaluation. The studies described above suggest that the processing reflected by the P3b appears to be independent of that involved in responding to the stimulus.

1.25 THEORIES OF THE FUNCTIONAL SIGNIFICANCE OF THE P3B

Although Johnson's Triarchic Model (1986, 1988) is a psychological theory of the P3b it does not make suggestions concerning the functional significance of this component. Instead, it provides a description of the variables affecting the occurrence of the P3b and how they interact to determine P3b amplitude. The triarchic model is also difficult to generalise beyond the oddball task.

Two main contemporary theories have been proposed, on the basis of the effects of experimental variables, describing the possible functional significance of the P3b.

Context Closure (Verleger, 1988)

Verleger proposes that the repetitive, highly structured tasks used in ERP research produce a situation which is favourable for the elicitation of the P3b. He proposes that the subjects combine successive events into larger units (meaningful contexts)

and that the events closing each of these units elicit the P3b. Verleger proposes that in addition to perceiving each stimulus and responding appropriately to it, the subjects also maintain an internal template of the context which includes an expectancy of the event which will close the context. When the expected stimulus is presented ('expectancy' is defined by Verleger as awaiting the closing stimulus) the stimulus is evaluated and responded to appropriately and the present context is closed. The P3b is thought to be an index of context closure. Closure of a cognitive epoch was first proposed as a functional explanation of the P3b by Desmedt and Debecker (1979) who suggested that the P3b reflected inhibitory input of the prefrontal cortex to the activating reticular formation. Verleger, however, suggested that the P3b was generated in the parietal cortex in areas involved in the integration of information in perception ("tertiary zones" of Luria, 1973). The P3b was thought to reflect the deactivation of these areas, where deactivation was defined as "the release of excess activation that has been previously accumulated in those areas". Verleger emphasises that the P3b is not a direct reflection of the information processing described as context closure, rather it reflects a closely following physiological process and so is indirectly related to it.

Context Updating (Donchin, 1981; Donchin and Coles, 1988)

In a similar vein to Verleger, Donchin and Coles (1988) suggest that the P3b is not a direct reflection of a cognitive process but appears to reflect a byproduct of the activation of a neural process involved in information processing. They suggest that the P3b is a "manifestation on the scalp of brain activity that performs a specific information processing function. The activity may occur in a number of different structures concurrently in a complex pattern". The core idea in the Context Updating theory is that P3b is an index of "strategic" as opposed to "tactical"

information processing. "Strategic" information processing refers to planning and control of behaviour which will affect responses to future stimuli, whereas, the parallel "tactical" processing involves selection of specific responses and actions to immediate stimuli. It was suggested that on repetition of relevant stimuli some adjustment is made in the information processing system establishing that no further response is required. Pribram and McGuiness (1989) referred to this adjustment as "context updating".

Donchin (1981) suggests that the P3b indexes this process of updating a schema or neuronal model. Donchin likens the schema to "a large, complex map representing all available data about the environment". Donchin suggests that some of the information may have just been received and so may be in some kind of working memory or short term memory, whereas other information may be in long term memory and so has to be retrieved and integrated into the schema. When unexpected but relevant events occur, the schema requires updating. This is achieved by the incorporation of the incoming information into the schema. It is this updating process which is thought to be indexed by the P3b. Without updating of the schemas an accurate representation of the environment cannot be maintained (Donchin and Fabiani, 1992).

Donchin and Fabiani (1992) suggest that context updating involves the marking of the attribute(s) of an event which made it distinctive from other events which had occurred. The authors propose that the updating process provides useful retrieval cues and therefore benefits subsequent recall of that event. The amplitude of the P3b is suggested to vary with the extent of updating and therefore to predict subsequent recall of the event. Donchin's group have reported a number of studies whose results appear consistent with this suggestion. Karis et al. (1984) visually

presented sequences of words to be subsequently recalled among which were occasional deviant words (larger font size). Through investigation of the single trial ERPs it was found that deviant words which were subsequently recalled had elicited larger amplitude P300s on initial presentation than those which were not recalled. This effect was only found for subjects using rote memory strategies, not those who adopted elaborative strategies. Fabiani et al. (1986) used a paradigm which minimised the use of elaborative strategies. Oddball tasks were presented to the subjects in which the rare stimulus had to be counted. Immediately following one of the oddball tasks the subject was asked to recall freely as many of the items from that sequence as possible. The subject had been unaware that memory for the items would be tested, therefore elaborate memory strategies should not have been used. As in the study of Karis et al., larger amplitude P3bs were elicited by items which were subsequently recalled.

Although the waveforms reported in these studies show a clear difference in amplitude of the P300 deflection elicited by stimuli that were subsequently recalled and those that were not, this amplitude difference does not appear to be restricted to parietal sites. The P3b has a maximal amplitude over parietal sites, therefore if the apparent memory effect was due to an effect on the processes reflected by the P3b, the change in amplitude would be expected to be maximal over parietal sites. In the studies of, for example, Karis et al. (1984) and Fabiani et al. (1986) the change in amplitude appeared to be present at all three electrode sites, although it was larger over central and parietal sites than over frontal sites. Donchin does not make any suggestions concerning the nature of the system involved in context updating. He suggests that the aim of the model is to provide a theoretical basis to stimulate predictive studies in an attempt to understand the functional significance of the P3b. These studies would extend present knowledge of the P3b obtained from

investigations of the experimental variables affecting the elicitation of the component.

To summarise, both the context closure and context updating theories were proposed, post hoc, to provide possible functional accounts of the P3b based on data concerning its antecedent conditions. Both theories, therefore, appear to be able to account for the present experimental data. The reason this is possible is that both theories are quite vague and general which makes it difficult to test specific predictions from them. The major difference between the two theories is that Verleger suggests that P3b is elicited when an expected stimulus is presented, whereas Donchin and Coles propose that a P3b is elicited when the schema of the current context requires revision because of the presentation of an unexpected or distinctive event. Knowledge of whether subjects expect or do not expect the rare P3b eliciting events is therefore crucial for evaluating the plausibility of these two theories. Donchin presents evidence in favour of the rare stimuli being unexpected but Verleger cites the "gamblers fallacy" (predicting an alternation after a run of one stimulus even though the subject knows the probability on each trial is 0.5) as evidence of the rare stimulus being expected. More systematic studies of the relation of expectancy to the P3b are necessary.

More specific criticisms can be made of both theories. The evidence of lesion studies (see section 1.22) question Verleger's suggestion of the neuronal basis of the P3b. Verleger suggested that the P3b was being generated in superior parietal regions. The study of Knight et al. (1989) showed that lesions in the superior parietal cortex had no effect on the amplitude of the P3b. The major criticism of Donchin's theory is that it consists of a number of assumptions which appear not to be based on firm evidence. They suggest that rare stimuli require updating of

context and that this, through the provision of retrieval cues, facilitates subsequent recall of that event. They suggest that this updating process occurs when distinctive events are presented. The P3b is also suggested to occur in response to distinctive stimuli and that P3b amplitude can be used as a measure of the distinctiveness of an event. As more distinctive events will cause greater context updating and therefore facilitate recall of that event, amplitude of the P3b will predict recall of the event. A relation has been reported between the amplitude of the P3b and subsequent recall of the eliciting event. This has been taken as support for the theory. However, no independent measure of distinctiveness has been made, the events eliciting the P3b were considered to be distinctive because of their low subjective probability. Some other characteristic of the eliciting events, other than distinctiveness, may be causing the elicitation of the P3b. In addition, the major evidence for Donchin's proposals, concerning changes in the amplitude of the P300 deflection depending on whether the item is subsequently recalled or not, does not appear to be restricted to the P3b.

The main problem with theories attempting to explain the functional significance of the P3b is that in order to account for the multitude of findings, the theory has to be fairly general. The large number of different paradigms in which the P3b has been elicited suggests that it may not be possible to explain the P3b in terms of one particular psychological process but that instead it may be reflecting the activity of a more general physiological process. This possibility is discussed in the next section.

1.26 IS THE P300 COMPLEX SIGNALLING THE ACTIVITY OF A GENERAL PHYSIOLOGICAL PROCESS?

As mentioned above, it may not be possible to explain the P3b in terms of one particular psychological process but an explanation in terms of a more general physiological process, which is necessary or involved in a number of different psychological processes, may be required (e.g. Pineda et al., 1989). This latter suggestion is supported by reports of P300-like potentials, recordable with similar latency, in a number of different areas of human and animal brains, e.g. the cingulate gyrus (Gabriel et al., 1983), suprasylvian and marginal gyri (O'Connor and Starr, 1985), hippocampus and amygdala (Halgren et al., 1980) and thalamus (Yingling and Hosobuchi, 1984). It is possible that a widely distributed neuronal system which synchronously acts on a number of areas of the brain may be involved in the generation or modulation of the P300 complex (this is consistent with the suggestion of Donchin and Coles (1988) that the P3b may be an index of information processing which may occur in a number of different structures concurrently).

One system showing the necessary anatomical, physiological and functional properties for the generation or modulation of the P300 complex appears to be that part of the noradrenergic system arising from the locus coeruleus (see Foote et al., 1983 for review). The diversity of projections of the dorsal noradrenergic bundle arising from the locus coeruleus suggests that it could have a modulatory effect on many different processes occurring at its terminal regions. Stimulation of this part of the noradrenergic system has been found to decrease background activity relative to stimulus elicited activity in neurons of the auditory, visual and somatosensory cortex and has similar effects on hippocampal cells. Noradrenaline (NA) is therefore thought to increase the 'signal-to-noise ratio' of information entering the

respective brain region and so facilitate processing. It has been suggested that the release of NA from the locus coeruleus modulates the responsiveness of the organism to biologically relevant events whilst in a waking state and particularly whilst in a state of increased attentiveness (Aston-Jones et al., 1984; Foote and Morrison, 1987).

Pineda et al. (1989) found that lesioning of the locus coeruleus and ascending noradrenergic pathways in the monkey led to a reduction in the amplitude of a scalp-recorded P300-like potential to rare tones (presented with a probability of 0.1 among frequent tones of probability of 0.9) but had little effect on other components in the waveform. This finding suggested that the integrity of the locus coeruleus-noradrenergic system was necessary for the elicitation of the monkey P300-like potential. Lesioning of the locus coeruleus and dorsal noradrenergic bundle would have also caused damage to other brain regions and systems making unequivocal interpretation of the results difficult. A subsequent study (Pineda et al., 1991) provided further support for the role of the locus coeruleus-noradrenergic system in generating P300-like potentials. Monkeys received injections of saline or clonidine (an alpha-2 adrenergic agonist which was thought to suppress locus coeruleus activity at the 3 doses used). The P300-like potential elicited in the auditory oddball task described above showed a dose-related decrease in amplitude in the clonidine condition. Amplitude of the P300-like potential returned to normal levels in a post-drug testing session.

The results of the studies reported by Pineda suggest a critical role for the locus coeruleus-noradrenergic system in the generation of P300-like potentials in the monkey but whether these results are generalisable to human P300 potentials is yet to be seen. A study on humans conducted by Clark et al. (1989) suggested that

noradrenaline and dopamine were involved in facilitation of the disengagement of attention which, as will be seen in section 1.28, bears similarities to the proposed functional significance of the P3a component in humans.

It is probably more realistic to think of NA as one of several neurotransmitters whose release is necessary for the occurrence of processing reflected by P300-like potentials. An example is provided by the study of Harrison et al. (1988) in which bilateral lesions of the septal nuclei in cats caused P300-like potentials to disappear. These lesions produced a marked depletion of acetylcholine (AChE) in the hippocampus. The results of the study suggested that the integrity of the septo-hippocampal cholinergic system was critical for the modulation of these potentials. Another study suggested the role of the serotonergic system in P300 generation (Ito et al., 1990). Ito et al. (1990) measured cerebral spinal fluid concentrations of the serotonin metabolite 5-hydroxyindoleacetic acid 5-HIAA and the dopamine metabolite homovanillic acid HVA in patients with Alzheimers dementia (DAT). ERPs were also recorded in the patients during a two stimulus auditory oddball task. The amplitude of the P300 elicited by the targets in the oddball task was significantly reduced and the latency prolonged in the patients compared with healthy age matched controls. P300 amplitude was significantly correlated with 5-HIAA concentration but not HVA concentration which led the authors to suggest that the serotonergic system was modulating the P300 component in these patients.

In summary, present knowledge does not give a clear indication of the role of neurotransmitter systems in the generation or modulation of the P300 complex. However, studies in animals suggest that the integrity of these systems appears necessary for the generation of P300-like potentials. This leaves open the possibility

that the P300 complex (or components of it) may be reflecting a facilitation of processing in certain brain regions rather than a specific psychological process.

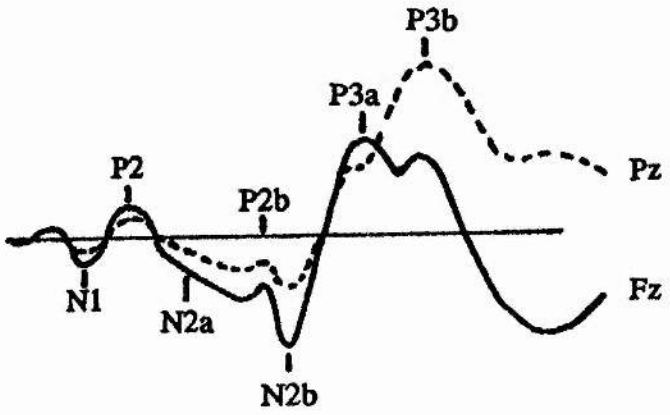
1.27 OTHER ERP COMPONENTS ELICITED IN THE ODDBALL TASK

A number of other mesogenous/endogenous ERP components are elicited by rare target and non-target stimuli in oddball paradigms (and were measured in the series of experiments reported here). Understanding the functional significance of these other components may help elucidate the psychological processes to which the P300 components are related. The components are illustrated schematically in figure 1.1 and will be considered in chronological order.

N100

The N100 is not a unitary phenomenon, the peak obtained in the ERP waveform resulting from the overlap of several components with different cerebral generators. Naatanen and Picton (1987), in a review of the component structure of the N100, have identified what they consider to be three 'true' N100 components which are dependent on the physical and temporal aspects of the stimulus and the level of arousal of the subject. Three other components have been identified which depend more on the conditions in which the stimulus occurs rather than its physical characteristics. Although these longer lasting components are not part of the N100 complex they do overlap the N100 latency region and so may affect the amplitude of the N100 obtained in the waveform.

Figure 1.1 Schematic illustration of the suggested component structure of the ERP to a deviant stimulus under detection conditions. The time range involving the greatest overlap of components (N1-N2b) is stretched for illustrative purposes. N2a refers to the MMN and P2b to the P165 component.



(Redrawn from Naatanen R. and Gaillard A.W.K. (1983))

The first 'true' component identified by Naatanen and Picton (1987) was a frontocentrally distributed negativity, with a latency of 100 ms, generated by bilateral vertically oriented dipoles in the auditory cortex of the supratemporal plane. Evidence for this component has been provided by magnetoencephalography (MEG) studies (e.g. Hari et al., 1980) and the work of Scherg and Von Cramon (1986) modelling dipoles which could account for the distribution of electrical activity recorded from the scalp. Rogers et al. (1990) present MEG data suggesting that component 1 of the N100 does not appear to be generated by a single stationary dipole source but is due to progressive excitation of adjacent cortical columns starting in the primary projection area and moving forward towards the association areas. The second component was originally described by Wolpaw and Penry (1975) and consists of a positive peak at 100 ms and a negative peak at 150 ms. It is thought to be generated in the auditory association cortex of the superior temporal gyrus. This component has been modelled by Scherg and Von Cramon (1985, 1986) and is consistent with findings from intracerebral recordings (Celesia, 1976; McCallum and Curry, 1979). Due to the radial orientation of the dipole generating this component, it can not be recorded by MEG. The third component of the N100 complex is a negative peak with a latency of 100 ms recorded maximally from the vertex and which often overlaps the slightly more anterior component 1 of the N100 complex. The existence of this component is suggested by intracerebral recordings (e.g. Velasco et al., 1985; Velasco and Velasco, 1986) and the MEG findings of Hari et al. (1982). The generator location of the third component is unknown.

The other components which have been identified as overlapping the N100 include the mismatch negativity (MMN) (see section 1.28) which is thought to be generated in the same region of the brain as the first N100 component but by different neuronal processes. Another component proposed by Naatanen and Picton (1987) is a

sensory specific 'processing negativity' which has an onset latency of 50-100 ms and continues while an attended auditory stimulus is processed. It is probably generated in the auditory sensory and association areas on the supratemporal plane and lateral temporal lobe. The final component is a second component of the processing negativity which Naatanen and Picton (1987) propose is generated in the anterior frontal cortex because it receives information from the auditory association cortex and feeds back to these areas to bias particular kinds of auditory processing. This component was proposed due to the results of scalp distribution studies of Hansen and Hillyard (1980) and cerebral blood flow studies of Roland (1981, 1982) and Roland et al. (1981).

The N100 components are responsive to change from one level of physical energy to another and so are sensitive to the transient aspects of stimuli (Graham, 1979; Loveless, 1983; MacMillan, 1973). The N100 generators may not be specifically involved in perception. It has been suggested by Naatanen (1986) that the N100 components, equivalent to components 1 and 3 identified by Naatanen and Picton (1987), may act as nonspecific attention triggering processes which cause the brain to become conscious of stimulus information extracted by earlier processes. It is possible, however, that the process generating the N100 is the result of an attention trigger rather than the trigger itself. It is suggested by Naatanen and Picton that an alternative interpretation of component 1 of the N100 complex is that it reflects the formation of a trace of the eliciting stimulus in auditory sensory memory. This suggests that the same neurons would be involved in the generation of the N100 and the MMN, the latter reflecting the detection of a mismatch between sensory input and the trace held in sensory memory of previous stimulation. Naatanen and Picton (1987) suggest that according to this hypothesis component 1 of the N100 would be determined by the physical properties of the stimulus and the timing and physical

properties of the previous stimuli which determine the refractoriness of the N100 neurons. If a stimulus identical to that represented by the trace is presented, only a small N100 will be produced because the stimulus will affect mainly neurons which are refractory. If a different stimulus is presented the N100 amplitude will be larger because the stimulus will affect neurons which are less refractory. In the latter case the trace formation process elicited by the stimulus is stronger and a new trace developed. Component 1 of the N100 is thought to be fully recovered after 4-5 s which is equivalent to the ISI at which the MMN can no longer be elicited. This finding is consistent with Naatanen and Picton's (1987) hypothesis because when the N100 neurons are fully recovered no MMN can be elicited. Naatanen and Picton (1987) suggest that the three functions which they propose for the first component of the N100 i.e. call of attention to stimulus information, reading out sensory information from the auditory cortex and forming a trace in auditory sensory memory may be carried out by different subpopulations of N100 neurons. The functional significance of the second N100 component is not known. Naatanen and Picton (1987) suggest that the third component may be involved in producing widespread transient arousal of the organism facilitating sensory and motor responses to the eliciting stimulus and putting the organism into a more efficient state.

P165 and P200

Following the N100, all tones in an auditory oddball task have been found to elicit a positive deflection irrespective of whether the stimulus sequence was being attended or not. This has been labelled the P200 (Goodin et al., 1978). A slightly earlier ERP component which Goodin et al. labelled the P165 was found only in response to

attended rare tones. These components will be discussed in more detail in the discussion of Chapter 4.

Mismatch Negativity (MMN)

The next negative deflection to occur in the ERP waveform after the N100 has been labelled the N2. Two negative components have been found to contribute to this deflection, the mismatch negativity (MMN) and the N2b. When the stimuli are attended, measurement of the MMN is difficult because of the overlap of the N2b component which is not present when the stimuli are ignored. When the stimuli are attended it is, therefore, difficult to determine whether the change in amplitude of the N2 deflection is due to a change in the MMN or N2b. The MMN however, has a more anterior scalp distribution than the N2b; shows reversal of polarity across temporal regions when referred to a nose reference, and, unlike the N2b, can be recorded by MEG. This means that in some situations it is possible to distinguish between the two components. Naatanen and Gaillard (1983) provide a good review of studies dissociating the MMN and N2b. In the present section and section 1.28, I will therefore only briefly summarise the main findings concerning these two components.

The MMN is the earlier of the two components occurring within the N2 time range. The MMN is an anteriorly distributed ramp-like component. It has a peak latency of approximately 200-300 ms but may occur later with small stimulus deviations or earlier with large deviations. The duration of the component is dependent on the size of the stimulus deviation.

The MMN is thought to reflect "an automatic pre-perceptual cerebral mismatch process" (Naatanen and Gaillard, 1983) which occurs whenever there is a change of stimulus in a repetitive sequence of homogeneous stimuli. The mismatch process is therefore similar to that proposed by Sokolov (1975) to trigger the orienting of attention to deviant/novel stimuli (this will be discussed further in section 1.28). The mismatch is proposed to occur between a passive sensory memory trace of the frequently occurring stimulus and the physical features of the presented stimulus. The MMN is thought to depend on deviance in physical features of the stimuli (e.g. intensity changes, N. Squires et al., 1975; Naatanen et al., 1978, 1981; changes in inter-stimulus-interval duration, Ford et al., 1976; Ford and Hillyard, 1981) but to be independent of factors such as meaning, significance or other psychological aspects of the stimuli (e.g. Naatanen et al., 1978).

The mismatch process is thought to be modality specific. Simson et al. (1977a) suggest differences in topography of the components in the N2 region depending on whether they are elicited by auditory or visual stimuli. In addition, ease with which an MMN can be elicited differs between modalities. The MMN appears to be a robust phenomenon in the auditory modality but appears extremely difficult to obtain in the visual modality, although recent studies (Woods et al., 1992; Alho et al., 1992) report a visual MMN. Naatanen and Gaillard (1983) suggest that the apparent modality specificity of the MMN and its scalp topography suggests that it may be generated in secondary sensory areas. The differences between the visual and auditory modalities in eliciting the MMN may be due to the nature of processing in the two modalities.

The MMN is sensitive to probability, being larger when the deviant stimulus probability is small (Naatanen and Gaillard, 1983) and is also sensitive to sequence

effects (Sams et al., 1984). The effect of sequence on the MMN will be discussed in more detail in chapter 10.

The independence of the MMN from attention is a current area of debate. Naatanen (1990) has suggested that the MMN reflects the outcome of a preattentionally detected mismatch between the presented stimulus and a sensory memory trace of recently presented stimuli. A study of Woldorff et al. (1991), however, has suggested that the MMN produced by intensity changes is affected by attention. As this is a key concept of Naatanen's Theory of automatic and controlled processing of auditory stimuli, I will postpone further discussion until section 1.28 where Naatanen's Theory is fully described.

N2b

The N2b is the second negative peak in the N2 time range and is superimposed on the MMN. The N2b has a sharper peak than the MMN and a central scalp distribution. It is not modality specific. The peak latency and duration of the N2b appears to be more fixed than that of the MMN, e.g. Renault et al. (1982) reported an MMN to stimulus omission whose duration was strongly correlated with reaction time and a following sharper negative peak (N2b) whose duration was constant and did not change with reaction time.

The N2b only occurs in response to deviant stimuli which are attended. In conditions in which the subject ignores the presented stimuli (e.g. reads) only an MMN occurs in the waveform, whereas when the stimulus sequence is attended both an MMN and an N2b are elicited. An N2b can occur in ignore conditions but only when the stimulus deviance is large enough to be intrusive (Naatanen et al., 1982).

The N2b is not dependent on stimulus deviance as it can be elicited by single auditory stimuli after long inter-stimulus-intervals (e.g. Ritter et al., 1968) in addition to deviations in an attended sequence of stimuli. Like the MMN, the N2b is sensitive to the probability of the stimulus (e.g. Donald and Little, 1981). The N2b is followed by a P3a which together are thought to form a complex (e.g. Snyder and Hillyard, 1976) whose generator processes may be involved in elicitation of the orienting response (OR) (Naatanen and Gaillard, 1983). The possible functional significance of the N2b will be elaborated in the discussion of Naatanen's theory (section 1.28).

Processing Negativity (PN)

The processing negativity (PN) is a long duration negativity (Parasuraman, 1980; Okita, 1979) which overlaps the MMN and N2b in certain situations. It occurs in response to all stimuli in the attended channel of a dichotic listening task. The PN has been proposed by Naatanen (1982, 1985) to reflect a matching process between sensory input and a neuronal representation of the stimulus to be attended (relevant stimulus), labelled by Naatanen as the "attentional trace". Naatanen's proposals suggest that the amplitude and duration of the PN will be increased the more similar the sensory input is to that represented in the attentional trace. This has been supported by the findings of Alho et al. (1986) who showed the largest PN to relevant stimuli but also showed a PN to irrelevant stimuli which was larger the more similar the eliciting stimulus was to that represented by the attentional trace. Similarly, Hansen and Hillyard (1980) found that the amplitude of the Nd (the difference negativity found by subtracting the ERP elicited by the irrelevant stimulus from that elicited by the relevant stimulus) was smaller the smaller the

separation in pitch between the relevant and irrelevant tones. The Nd was also found to have a longer onset latency for smaller pitch differences.

The PN will not be discussed very much in the rest of this thesis. As will be discussed in section 1.28, in a one channel oddball task, such as that used in the present series of experiments, access to attentional processing, allowing evaluation and identification of the stimulus, is proposed to be via the monitoring for a mismatch with the sensory memory trace (detection of which is reflected by the MMN). The PN reflects an alternative route to attentional processing involving controlled processing which maintains a neuronal trace of the features of relevant stimuli so that the occurrence of a match triggers further processing of the stimulus.

Slow Waves

Following the P3b, a frontal negative and parietal positive deflection have been found in the ERP waveform. These deflections were originally thought to reflect the activity of a generator whose equivalent dipole lies tangential to the upper surface of the brain. Experimental evidence, however, has suggested that they are separate ERP components (e.g. Loveless et al., 1987), now referred to as the frontal negative slow wave and parietal positive slow wave respectively (e.g. Picton and Stuss, 1980). Although the slow waves are elicited under very similar conditions to the P3b, a number of studies have provided evidence of a dissociation between these components (e.g. Ruchkin and Sutton, 1983; Ruchkin et al., 1980a). The slow waves will be discussed in more detail in the discussion of Chapter 4.

1.28 NAATANEN'S THEORY OF THE ROLE OF ATTENTION IN AUDITORY INFORMATION PROCESSING

Theories concerning the possible functional significance of the P3b have been described in section 1.25. Due to the comparative lack of studies of the P3a, there does not appear to be a specific theory concerning its functional significance. Naatanen (1990), however, presents a theory of controlled and automatic auditory processing, based on ERP findings, which includes a description of possible processes leading up to and including the elicitation of the P3a component in a one channel oddball task such as that used in the experiments reported in this thesis. This part of Naatanen's model is summarised in Figure 1.2. The second part of Naatanen's model concerning parallel controlled processing as an alternative route to access attentional processing will not be discussed in detail here. Naatanen (1990) does not consider the controlled processing route to be that used for target detection in a one channel auditory oddball task as he suggests that the target stimuli do not occur frequently enough for an attentional trace of their physical features to be maintained. Before reviewing Naatanen's theory I will briefly define some of the terms he uses.

(1) Automatic processing: is that which occurs unintentionally, preconsciously and without interference from other concurrent processes (Posner and Snyder, 1975a and b).

(2) Preattentive/preattentional processes: processes prior to those whose results can be consciously reported.

(3) Neuronal trace: representation of prior stimulation encoded in some way by the neurons. Naatanen is referring specifically to short duration neuronal representations of physical features of stimuli.

(4) Selective Set: refers to an experimental paradigm in which the subject is prepared for a particular stimulus and is instructed to indicate by making a response that they have detected or recognised the stimulus. The subject chooses which of several stimuli to expect or search for rather than which of several actual stimuli to analyse (see Kahneman and Treisman, 1984).

(5) Attentional set: see selective set

(6) Attentional Trace: A trace of the features of stimuli which is actively maintained by the subject through rehearsal.

(7) Controlled Processing: processing of stimuli which does not occur automatically.

(8) Attentional discrimination: processing of the stimulus resulting in its discrimination and identification which is available for conscious report.

(9) Limited capacity processing: processing which only has a limited amount of resources available at a certain time. If these resources are required for two tasks simultaneously, less processing will be carried out of the stimuli in both tasks than if either task was completed alone.

(10) Executive Processes: limited capacity processes following sensory analysis of stimuli.

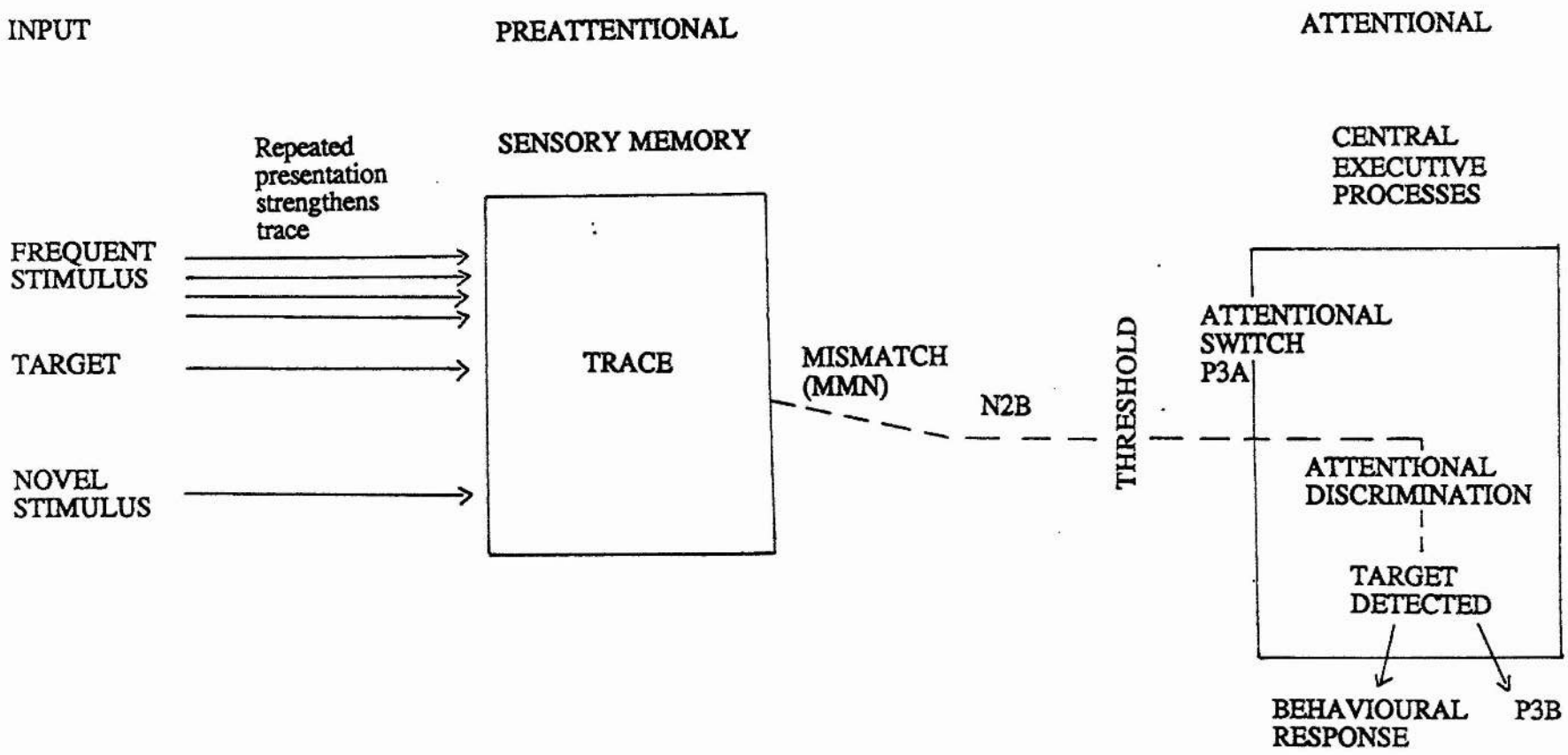


Figure 1.2 Illustration of automatic route involved in auditory processing proposed by Naatanen (1990).

The automatic processing route

Naatanen proposes that attentional discrimination of stimuli is intiated by a preattentional process which detects a mismatch between the physical features of the presented stimulus and a passively formed sensory memory trace representing the physical features of recent stimulation.

It is suggested that on repeated presentation of a frequently occurring stimulus a trace of its physical characteristics is passively formed in sensory memory. If a rarely occurring stimulus is then presented, for example, a target or a novel sound, its physical features will not match those held in the sensory trace and so the process reflected by the MMN will be elicited indicating the occurrence of a mismatch. Occurrence of the mismatch process causes the activation of another process which is reflected on the scalp by the N2b. If the N2b process is activated to a certain extent, it overcomes a threshold and causes an attentional switch so that the presented stimulus is processed by the attentional central executive mechanisms. The strength of the N2b process is determined by the size of the mismatch which depends on the strength of the trace in sensory memory and on the magnitude of deviation of the presented stimulus from the trace. The attentional switch is thought to be reflected by the P3a component. If processing by the central executive mechanisms causes detection of a target, the appropriate response is made and the process underlying the generation of the P3b is elicited.

The model suggests that if (as proposed by Naatanen, 1990) this is the route to attentional processing taken by stimuli in the auditory oddball task, then the

occurrence of both the P3a and the P3b depends on the detection of a mismatch between the presented stimulus and a trace of the frequently occurring stimulus.

Naatanen (1990) suggests that traces of two or more stimuli can exist simultaneously in sensory memory; this is supported by findings of Sams et al. (1984). On presentation of a rare stimulus a mismatch is detected between its physical features and those held in the sensory memory trace, in addition a weak trace of the presented stimulus also forms in sensory memory. Sams et al. (1984) showed that the presentation of a rare stimulus, preceded by the presentation of an identical rare stimulus, produced a smaller MMN than the same rare stimulus preceded by several nonidentical stimuli. This was because in the former condition a trace of the rare stimulus was still present in sensory memory when the same stimulus was next presented. When a frequent stimulus was presented, after the presentation of two rare sounds, a small MMN was produced in response to the frequent because although its physical features matched those held in the sensory trace of the frequent stimulus, they mismatched with those held in the sensory trace of the rare sounds. These findings suggest that the absence of a trace in sensory memory for a particular stimulus is probably due to its decay over time rather than its displacement from sensory memory by a trace of a different stimulus.

According to Naatanen, the effect of attending to the sequence of stimuli in a one channel oddball task, compared with ignoring the stimulus sequence and engaging in a different task, occurs at the level of a facilitatory coupling between the central executive processes and the mismatch process. That is, an attentional set is formed 'waiting' for the occurrence of a mismatch. The mismatch process is thought to be automatic, occurring in response to rare stimuli whether or not they are being attended. In ignore conditions, however, where the subject has to engage in another

task (e.g. reading) while the stimuli are presented, the subsequent processes reflected by the N2b, P3a and P3b are not elicited. It is proposed by Naatanen (in prep) that the temporary 'facilitatory coupling' may occur between the MMN and N2b generator processes. The more facilitation, the easier it is for the MMN process to trigger the N2b process and thus call attentional processing of the presented stimulus. When subjects are ignoring the stimuli, the facilitatory connection between the MMN and N2b processes will not be present and it will therefore be more difficult for the MMN to trigger the N2b process. In the ignore case therefore it will only be very deviant stimuli, which elicit large mismatches with the presently held sensory trace, that will trigger attentional processing of the stimulus.

A potential problem for Naatanen's theory of automatic auditory processing

A central proposal of Naatanen's theory is that the mismatch process, activated when an incoming stimulus does not match the features represented in the sensory memory trace, is strongly automatic. This suggests that an equivalent sized MMN would be elicited in response to rare stimuli whether the sequence was being attended or ignored.

One problem with previous experiments is that a strong selective set may not have been established in experiments investigating the effects of attention on the MMN and N2b. In dichotic listening experiments reported by Naatanen's group, the rate of stimulus presentation has been slow which is known to make selective focussing of attention difficult (Naatanen et al., 1978, 1980) and in single channel experiments the ignore conditions have often involved reading a book which again did not involve highly focussed attention. Woldorff et al. (1991) carried out two dichotic listening experiments which optimised selective attention. The first experiment

involved the presentation of tones at 120-320 ms ISIs. Deviant tones (tones of lower intensity) in both the attended and unattended channels elicited negative deflections consistent with the previously reported MMN. The MMN produced by the unattended input, however, was very much reduced in amplitude compared with that elicited by the attended deviant stimuli and the MMN elicited in previous experiments. A second experiment presented stimuli at a shorter ISI (65-205 ms) and found that the deviant stimuli in the unattended input elicited a negligible MMN whereas that elicited by attended deviants was consistent with previous reports. The amplitude difference between conditions, of the negative deflection in the N2 latency region, was attributed to a decrease in amplitude of the MMN in response to the unattended stimuli rather than the overlap of an N2b in the attend condition. The N2b is thought to have a slightly longer onset latency than the MMN which suggests that if the difference in amplitude between the attended and unattended MMN is due to the overlap of an N2b in response to the attended rare stimuli, the difference in amplitude would be expected to have a later onset than the MMN. In the Woldorff et al. study the N2 deflection had the same onset time in response to both attended and unattended stimuli. Woldorff et al. suggested that these results provided evidence that "the processing of stimuli in unattended channels can be attenuated or gated at an early sensory level under conditions of highly focused auditory selective attention".

Naatanen (1991) agreed that the Woldorff et al. finding was important but suggested that the size of the effect was smaller than that suggested by Woldorff et al. and was partly due to the overlap of other ERP components such as the N2b in the attend condition. The difference wave (subtracting the response to the frequent stimulus from that to the deviant stimulus) showed a larger amplitude at central than frontal sites which according to Naatanen indicated the presence of an N2b as the MMN has

a more anterior distribution. As a very short ISI was used, Naatanen suggested that the rare stimulus occurred frequently enough for an attentional trace to be maintained by controlled processes. The larger negativity in the MMN latency region could therefore have been partially produced by the contribution of a processing negativity (PN) elicited when the rare stimuli matched an attentional trace. To investigate this possibility, Naatanen (1991) conducted a dichotic listening study using a rapid rate of stimulus presentation. Within the input stream to each ear were two deviant stimuli (change in frequency or intensity). The task required one of the deviant stimuli, in a designated ear, to be counted. By comparing the response to the non-target deviants between the attended and unattended stimulus streams it was possible to avoid the problem of PN overlap associated with attended targets. The MMN produced by attended intensity changes was found to be larger than that in the unattended channel. The MMN to frequency changes appeared to be of the same amplitude to attended and unattended stimuli. Naatanen therefore disagreed with the interpretation given of Woldorff's results. He suggested that as no suppression of the MMN was found in response to frequency changes in the same sequence of stimuli in which a change in intensity, when unattended, caused a suppression of MMN, sensory mechanisms and storage functions must still be going on in response to unattended stimuli. Naatanen suggested that the effect was produced because of a suppressing influence on the intensity MMN generator rather than on antecedent sensory analysis and storage functions. Whether the MMN region of the waveform, in response to stimuli which are deviant in ways other than intensity, is affected by attention remains to be investigated. Naatanen (1991) suggested that the frequency MMN is not affected by attention.

Naatanen's Theory and the P3b

Naatanen (1990) does not specify the processes which may underlie the generation of the P3b but only suggests that the evaluation of the stimulus by the central executive mechanisms is necessary before this component is elicited. Naatanen's theory is not inconsistent, therefore, with the context closure or context updating hypotheses which suggest possible processes that the P3b may be indexing. For example, the context updating hypothesis assumes that evaluation and identification of the stimulus is necessary before a P3b is elicited and that the component reflects processes involved in updating of a neuronal model of the environment. The theories of Naatanen and Donchin are therefore complimentary. Naatanen's model provides a possible route to attentional processing of a presented stimulus and its detection as a target in a certain experimental task. Donchin's context updating hypothesis suggests the possible processes which may be reflected by the P3b elicited once the target has been detected. Naatanen's theory appears to be limited to some extent in that it offers possible explanations for the route to the elicitation of the P3b only in the paradigms used by his group to investigate the MMN and PN.

The controlled processing route

The alternative route to attentional processing proposed by Naatanen (1990) involves controlled processing occurring in parallel with the automatic processing discussed above (this route is not shown in figure 1.2). This route was discussed briefly in section 1.27 and involves the maintenance of an attentional trace. A match with the trace allows further processing of the presented stimulus (access to central executive processes). Naatanen suggests that this is not the route used for target detection in a one channel, two stimulus, oddball task. In contrast, a number of

other authors report that their results are suggestive of the involvement of a template matching process in the elicitation of the P3b. Thatcher (1977) presented subjects with sequences of stimuli consisting of (a) a number of random dot displays (b) a letter (c) a number of random dot displays (d) a letter which either matched or mismatched the first. Both the first and second stimuli elicited P300s but the second stimulus elicited a larger P300 if it was elicited by a match than a mismatch. Thatcher proposed that "The response to the match test stimulus reflects both a long-term memory match and a match with the recently activated letter representation". John (1977) similarly suggested that the P300 "is a general wave process reflecting the completion of a 'fit' between external sensory information and internal representational systems". Experimental results suggest, however, that this template is not necessarily a representation of the physical parameters of the stimuli. The target can be defined as a class of stimuli whose members differ physically (e.g. Courchesne et al., 1977; Friedman et al., 1978; Johnson and Donchin, 1978, 1980; Thatcher, 1976). Posner et al. (1973) showed that when signals are defined as physical mismatches, the mismatches elicit a larger P3b than matches.

1.29 POSSIBLE EXPLANATIONS, ARISING FROM NAATANEN (1990), OF THE PROCESSING INVOLVED IN ODDBALL TASKS

The one channel oddball task to which Naatanen refers is a two stimulus oddball task. Naatanen suggests that the target is detected by the monitoring for the occurrence of a mismatch between the presented stimulus and a passively formed trace of the frequently occurring stimuli. Detection of a mismatch triggers a switch of attention to the stimulus. This attention switch allows the stimulus access to

"executive processing" which leads to evaluation of the stimulus producing results which are available to conscious report.

The three stimulus oddball task is also a one channel task as all stimuli require attention. Naatanen (1990) would therefore predict that conscious discrimination of both categories of rare stimuli would be achieved via the passive route. Both categories of rare stimuli would mismatch with the passive neuronal trace of the features of the frequent stimuli. Detection of the mismatch would trigger an attentional switch which would allow executive processing to determine which stimulus requires a response.

When the sequence of stimuli is ignored, Naatanen argues that the neuronal trace of the frequent stimulus is still formed and the comparison process between the trace and the incoming stimulus still occurs. If a rare stimulus is deviant enough or attention capturing enough a mismatch will be detected and an attentional switch will occur to that stimulus. The threshold for the detection of a mismatch, however, will be higher than when the stimuli are attended to because attention to the stimulus sequence will set up a facilitatory link between the mismatch detector and the attention switching mechanism. When the sequence of stimuli is attended smaller mismatches will trigger further processing of the stimulus than when the stimulus sequence is not attended.

In dichotic listening experiments the stimuli in the unattended channel are processed in the same way as ignored stimuli discussed above. The stimuli in the ignored channel will therefore only gain access to conscious processing if they are very deviant from the frequent stimuli or particularly capture attention. Naatanen argues that, in order to attend to stimuli in one channel and ignore those presented in

another channel, an attentional trace is set up of the features which distinguish the stimuli to be attended from those not to be attended. This trace is actively maintained by rehearsal. When a stimulus matches the trace it gains access to the central executive processes which allows the stimulus to be identified consciously and the appropriate response made.

Naatanen argues that in order for the attentional route (detection of a match with trace of task relevant stimuli) to be used the stimuli must be presented frequently otherwise the trace cannot be maintained. He argues that in a one channel oddball task the targets do not occur frequently enough for an attentional trace to be maintained unless the inter-stimulus-interval (ISI) is very short (Naatanen 1991). The one channel oddball tasks to which Naatanen refers involved only two stimuli. It is possible that in a three stimulus oddball task the two categories of rare stimuli are treated together as one category of rare stimuli but this would depend on the probability of the stimuli and the rate of stimulus presentation. Only if the rare stimuli occur frequently enough would it be possible to maintain a trace of the features which distinguish the rare stimuli from the frequent stimuli. Both categories of rare stimuli would gain access to central executive processing which would then determine the target stimulus.

1.210 SUMMARY OF CURRENT KNOWLEDGE CONCERNING THE P3A

The aim of the experiments reported in this thesis was to expand the currently limited knowledge of the P3a by investigating the variables affecting the occurrence of this component. Before moving to the experimental sections I will briefly summarise current knowledge concerning the P3a.

The P3a is a component of the P300 complex which can be identified in the ERP waveform as a fronto-centrally distributed peak with a slightly earlier latency than the P3b. At present the fronto-centrally distributed P300 component has been reported in response either to rare stimuli randomly mixed with frequent stimuli when the sequence is ignored (Squires et al., 1975), or to rare non-target stimuli which are novel or deviant from the frequently occurring stimuli when the sequence is attended (Courchesne et al., 1975; Knight, 1984; Knight et al., 1989; Yamaguchi and Knight, 1991a). Like the P3b, the P3a appears to be elicited by stimuli in all modalities, although it is easier to elicit in the auditory and somatosensory than visual modality.

As the P3a appears to be elicited by rare unattended events or deviant or novel events in an attended sequence, it has been suggested by a number of authors that the P3a may be related to the orienting of attention.

Courchesne et al. (1975) suggest that the occurrence of the P3a depends on the stimulus being unrecognisable and unpredictable in its time of occurrence. The authors suggest that as the novel stimuli in their task were irrelevant and could not be recognised and categorised when presented, the P3a elicited by the novel sounds may be a sign of Pavlov's (1928) "what is it" response to novel or unrecognisable stimulation. Courchesne et al. point out that from the design of their experiment it is not possible to determine whether the P3a reflects the orienting or investigatory aspects of the response. Courchesne et al. also suggest the alternative hypothesis that unrecognisable stimuli elicit a frontally distributed P300, whereas recognisable stimuli elicit a posteriorly distributed P300. The authors suggest that the distribution

of the P300 elicited by the novel sounds become more posterior on repeated presentation because the stimuli become recognisable.

The first explanation of the P3a suggested by Squires et al. (1975) was that the component may reflect the activation of an additional set of neurons specific to the infrequent stimulus and which are not, therefore, in a refractory state. This does not, however, account for why decrements in loudness elicit a P3a since loudness is thought to be encoded by the number of neurons active and so a decrease in loudness would just activate less of the same set of refractory neurons. Squires et al. therefore suggest the alternative explanation that the P3a may be indexing a basic sensory mechanism which detects any change in a background stimulus, perhaps by detecting a mismatch with a specific neuronal model (the authors reference Sokolov, 1963) formed by repetition of a background stimulus. This possible explanation is virtually identical to that proposed by Naatanen in his model of automatic and controlled processing of auditory stimuli (1990). The explanations of Squires et al. and Naatanen differ only in the specificity of the predictions. Naatanen explicitly suggests that the neuronal model, against which the mismatch occurs, represents the physical features of the stimuli, whereas Squires et al. do not expand on the possible nature of the neuronal representation.

Knight (1984) has shown that the integrity of the prefrontal region is necessary for the elicitation of the P3a. Knight suggested that the decreased P300 in response to novel stimuli, in prefrontally lesioned patients, may be a reflection of abnormal external-internal integration because of defective prefrontal control over sensory-limbic systems.

The experiments to be reported in this thesis were conducted to investigate the conditions under which the P3a did or did not occur, thereby, providing information necessary for understanding the functional significance of this component. An auditory oddball task, similar to that of Knight (1984) and Knight et al. (1989), was used in the present series of experiments as it has been reported to elicit reliable P3a and P3b components. The initial experiment was conducted to ensure that a dissociation between P3a and P3b could be obtained in our laboratory using different stimuli from those used by Knight et al.. Subsequent experiments investigated the experimental variables affecting the occurrence of the P3a. Naatanen's theory (1990) allowed a number of predictions to be made regarding the P3a and when it should or should not occur. These predictions were therefore used to guide the experiments reported here. Two main hypotheses were investigated throughout these experiments. The first was whether the P3a resulted from a mismatch detection process and, if so, in what way the eliciting stimulus had to differ from the frequent stimulus in order to elicit the P3a. The second hypothesis concerned the proposed relation between the orienting response and the processes reflected by the P3a.

CHAPTER 2

GENERAL METHOD

PARADIGM

The experiments reported here employed one basic paradigm which was manipulated in a systematic way to investigate the variables affecting the occurrence of the P3a component of the P300 complex. This task was the oddball paradigm of Knight et al. (1989) which involved monaural presentation of auditory stimuli at 1 s inter-stimulus intervals (ISI). The sequence of stimuli presented by Knight et al. (1989) consisted of the random mixing of 80% frequent tones, 10% target tones requiring a button press response and 10% 'novel sounds' which consisted of unexpected complex tones and environmental noises.

The task used in the experiments reported in this thesis was a slightly modified version of the task used by Knight et al.. Stimuli were presented binaurally to subjects at an inter-trial interval of 2 s. The slightly longer inter-trial interval was due to technical limitations on the speed of stimulus presentation and ERP acquisition. The inter-stimulus interval varied throughout the sequence because the novel sounds were of longer duration than the tones. The stimulus sequence consisted of the random mixing of 70% frequent tones, 15% target tones and 15% 'novel' sounds. As discussed in Chapter 1 (General Introduction), there is an inverse relationship between probability of a stimulus and the amplitude of the P300 deflection. In order to obtain a P300 of measurable amplitude, the targets and novel sounds were presented with a low probability. The probability was increased slightly from that used by Knight et al. (1989) in order to reduce the total number of

trials in the sequence whilst providing a sufficient number of trials to average for each infrequent condition. The 'novel' sounds used in the present experiments were different from those used by Knight et al. (1989).

STIMULI

The sequences of tones and 'novel' sounds were presented binaurally through headphones. The three tones used were generated by computer to have frequencies of 1000 Hz, 750 Hz and 500 Hz with rise and fall times of 10 ms and a duration of 50 ms. The 1000 Hz and 750 Hz tones are referred to as high and low tones in the following experiments. The 500 Hz tone was only used in experiment 2. The novel sounds were produced by recording short segments of environmental noises eg. car horns, duck quacks, footsteps, from a sound effects tape onto the computer using the Pro Sound Designer Gold package for the Amiga. The software package was then used to select a 100 ms segment of each sound with a fast onset and offset time. All stimuli had a peak loudness of approximately 85 dBA SPL.

SUBJECTS

The subjects of experiments 1, 2, 4A and 6 had no prior experience of the stimuli and experimental procedure used. One subject of both experiments 4B and 5, and two subjects of experiment 7, had previously participated in another experiment reported here. The procedure of experiment 3 was completed by 9 subjects in the same recording session as the procedure for experiment 2, the other 3 subjects completed the procedure for experiment 3 only.

RECORDING

For all experiments reported here recordings were made from either silver/silver chloride or tin electrodes placed at 9 scalp locations (Fz, Cz, Pz and positions 75% of the distance from the midline to F7, T3, P3, F8, T4 and P4 of the 10-20 system, Jasper (1958)). The silver/silver chloride and tin electrodes were never used in combination. All scalp electrodes were referred to linked mastoids with a ground electrode located on the head midway between Fz and Cz. Bipolar EOG was recorded from an electrode above the right eye and another beside the left eye. EEG and EOG were digitised at 250 Hz in epochs of 1024 ms, with a 100 ms prestimulus baseline (bandpass 0.03-30 Hz). Trials contaminated by EOG artifact were rejected before averaging.

PROCEDURE

Subjects were comfortably seated in an electrically shielded room in front of a desk to which the response button was attached. The headphones were positioned over the ears taking care not to dislodge or put pressure on the scalp electrodes. The practice trials were presented in order to familiarise the subject with the stimuli to which a response was required. Instructions regarding the task were given and will be provided for each experiment in the individual method sections. For all experiments, subjects were instructed to relax but to keep as still as possible during recording and to fixate a point on the VDU screen, positioned immediately ahead, in order to minimise eye movements. If subjects blinked on a large proportion of the practice trials they were asked to try to reduce the frequency of blinking during recording but not to allow this to affect their performance of the task. If few blinks were present during practice no specific instructions were given.

CHAPTER 3

GENERAL DATA ANALYSIS

Three deflections could be consistently measured in the experiments reported in this thesis. Labels were assigned to the deflections according to their polarity and mean latency in experiment 1. Amplitudes were measured against a pre-stimulus baseline of 100 ms and latencies were measured from stimulus onset to the peak of the appropriate deflection.

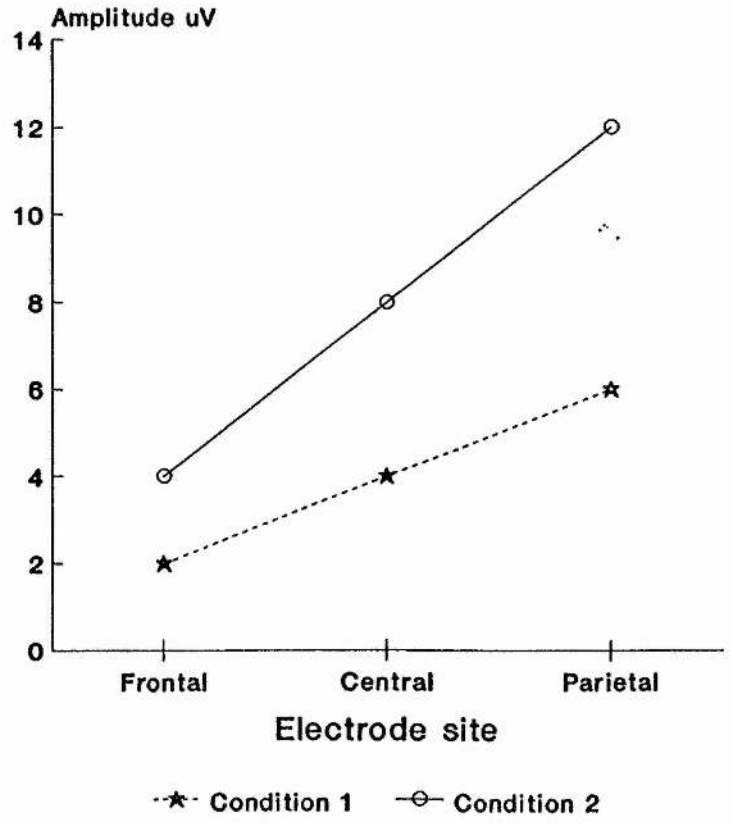
In order to reduce the influence of unresolved noise in the waveform, the statistical analyses were not carried out on the peak amplitudes but on the amplitude of the area of waveform +-12 ms round the peak of interest. This was determined in each subject by finding the latency of each peak at the site where measurement was easiest (details of this will be given for each experiment), determining the window +-12 ms round this peak and finding the mean amplitude of this area of the waveform for each electrode site.

In addition to the three deflections consistently obtained in the experiments, a sustained negative deflection was found at frontal sites and a sustained positive deflection was found at parietal sites between approximately 500 and 900 ms. As these deflections were of longer duration than those mentioned above, no definable peak was present to measure. In order to investigate this slow wave activity, statistical analysis was therefore carried out on the mean amplitude of the region of waveform between 500 and 900 ms.

To investigate the differences in amplitude of the peaks and the 500-900 ms region in the different experimental conditions, ANOVAs were carried out. These were generally of the form subject*condition*chain*site with subject and condition referring to the subjects and conditions in the experiment. In order to compare differences in amplitude between midline and lateral sites, and between hemispheres, the nine electrodes of the recording montage were divided into three chains of three electrodes, that is those over the left hemisphere, over the right hemisphere and over the midline. Therefore in the ANOVA, chain refers to the three chains of electrodes and site refers to the three electrode sites within each chain, ie. frontal, central and parietal sites. Details of the ANOVAs will be provided for each experiment individually. In cases where it was impossible to measure a peak, the mean latency window of the other subjects waveforms was used for that subject. Where necessary the Geisser-Greenhouse (1958) procedure was used in estimating the significance of the F ratios to control type I error associated with inhomogeneity of covariance (Keselman and Rogan, 1980).

ANOVA allows the investigation of amplitude differences across sites but can be misleading if used to investigate differences in scalp distribution. This is because differences in the amplitude of a component elicited under two conditions may suggest an apparent difference in scalp distribution which is not in fact present. For example, if the same neural generator is activated in two experimental conditions, but in the second condition the activity is twice that of the first, the component elicited in the second condition will be twice as large at each electrode site than that elicited in condition one. If amplitude of the components elicited in the two conditions is plotted against site, a graph like that in Figure 3.1 will be obtained. An ANOVA performed on these amplitude measurements would suggest a difference in scalp distribution between the two conditions (in the form of a condition by site

Figure 3.1. Graph showing that when the same generator is active in two conditions (here an imaginary generator oriented so that its activity is recorded maximally from parietal sites and least from frontal sites), an interaction will be obtained between condition and site when the generator is more active (producing a larger amplitude deflection) in one condition than the other.



interaction) which, because the same generator is active in each case, can not be correct. The problem occurs because the ANOVA is based on an additive model, assuming that if there is an increase in the strength of a generator a constant value is added on to the amplitude measurement at each site. Difference in source strength, however, has a multiplicative effect, so in the present example the amplitude would be doubled at each site. To overcome this problem in the experiments reported here the data was rescaled, using the method of McCarthy and Wood (1985) which eliminates absolute amplitude differences between conditions leaving the analysis to investigate the pattern of voltage differences across the scalp.

The effects of experimental conditions on both the amplitude and scalp distribution of an ERP component are of interest. Changes in scalp distribution between conditions would suggest a change in neural generator configuration, whereas changes in amplitude would indicate changes in the strength of the generator(s). In the analysis of the present experiments two ANOVAs were therefore performed for each component, one before and one after the data was rescaled.

To investigate further any interactions obtained from the ANOVAs the Newman-Keuls post hoc test was employed.

A NOTE ON P300 COMPLEX NOMENCLATURE

There have been several reports (discussed in Chapter 1) that the P300 is not a unitary phenomenon but can be dissociated into a number of components which overlap in time. This makes it difficult to label ERP deflections which are thought to be part of the P300 complex. Giving the same label to a positive deflection in the P300 latency range elicited by stimuli in two conditions may be misleading because

it would suggest that the same processing was occurring in the two conditions. It is possible that the two deflections instead reflect different components of the P300 complex (and perhaps different psychological processes). However, unless the components contributing to the deflection can be identified, a general label appears to be unavoidable.

In describing the waveforms in this thesis, all positive deflections, whose latency suggests that they are part of the P300 complex, will be labelled as P300 deflections. The relevant deflections usually occurred within 250-400 ms after stimulus onset. This general label will be used irrespective of the nature of the eliciting stimulus, the experimental condition or the scalp distribution of the deflection. The label will be used to indicate that the deflection reflects one or more components of the P300 complex.

In cases where the scalp distribution of the P300 deflections suggest a greater contribution of one P300 component to the waveform, additional labels (P3a and P3b) will be used to emphasise different effects of the experimental conditions or stimuli. A parietally distributed P300 deflection will be labelled the P3b whereas deflections with a more anterior distribution will be labelled the P3a. Some investigators have referred to P3a as a deflection having a maximum voltage at frontal and central sites. By contrast the label P3a is used here to refer to a deflection with a relatively anterior voltage distribution. Thus a deflection that is equal or more positive at central sites than parietal sites is a termed a P3a. These labels will be used to emphasis the differences between experimental conditions. The labels are not meant to infer exclusive contributions of one or other component to the P300 waveform. Indeed the system generating the P3b may also contribute to the more

anteriorly distributed P300 deflection. When differences in scalp distribution are not found between experimental conditions, the more general label of P300 will be used.

CHAPTER 4

EXPERIMENT 1: INVESTIGATING THE DISSOCIATION OF THE AUDITORY P300 COMPLEX

INTRODUCTION

As discussed in the General Introduction at least two dissociable positive components of the P300 complex have been identified in the visual, eg. Courchesne et al. (1975), auditory, eg. Squires et al. (1975), Knight (1984) and Knight et al. (1989), and somatosensory modalities, eg. Yamaguchi and Knight (1991). A parietally distributed P3b component has been identified in response to rare target stimuli and a more anteriorly distributed P3a component has been reported in response to certain rare deviant sounds.

The research reported in this thesis was concerned with the investigation of the variables affecting the elicitation of the P3a component of the auditory P300 complex, in order to identify the conditions under which it occurred and gain some understanding of its psychological significance. The paradigm manipulated throughout the experiments reported here was the oddball task used by Knight et al. (1989), in which a rare target tone and rare novel sounds were randomly interposed within a sequence of frequent tones. The experiment reported in the present chapter was carried out to ensure that the reported dissociation of the auditory P300 could be obtained in a slightly modified version of the Knight et al. (1989) paradigm (described in Chapter 2), using complex novel sounds different to those used by Knight et al.. It was predicted, on the basis of the results of the Knight et al (1989) study, that the rare target tones would elicit a parietally distributed P300 (P3b),

whereas the rare 'novel' sounds would elicit a more anteriorly distributed P300 (P3a) with a slightly earlier latency than the P3b.

METHOD

Subjects

Twelve healthy subjects (mean age 24, range 20-32 yrs, 8 female) were tested. All were paid volunteers.

Design

Subjects were presented with two 300 trial stimulus sequences. Both sequences consisted of a random mixing of a frequent high tone (P=0.70), a low target tone (P=0.15) and 30 different sounds (P=0.15). The sequences were the same apart from the order in which the different 'novel' sounds were presented. The order of the two sequences was balanced across subjects. Prior to the presentation of the experimental sequences subjects were presented with a practice sequence of 15 stimuli. This sequence included 9 frequent tones, 3 target tones and 3 'novel' sounds.

Procedure

Subjects were informed that a sequence of sounds would be presented through the headphones which would include a high tone and occasionally a low tone and other sounds. Subjects were instructed to press the response button as quickly as possible,

whilst avoiding errors, whenever they heard the lower of the two tones but to make no response to the high tones or the other sounds. Following successful completion of the practice trials each sequence of experimental trials was presented. The experimental sequences were split into three blocks of 100 trials with a 30 s break between each block. A break of approximately 2 minutes was given between the two sequences. Responses were made with the preferred hand.

DATA ANALYSIS

Grand average waveforms for the first and second sequence of stimuli are shown in Figure 4.1a and 4.1b. These waveforms were obtained by averaging together the ERPs produced by the twelve subjects.

Separate averaged waveforms were obtained for the three conditions for the first and second sequence of stimuli. The waveform produced in response to the frequent tones was averaged over a mean of 175 trials (ranging from 146-209 trials) for the first sequence and 170 trials (ranging from 90-207 trials) for the second sequence. The waveform produced in response to the target was averaged over a mean of 38 trials (ranging from 24-44 trials) for the first sequence and 38 trials (ranging from 29-44 trials) for the second sequence. The waveforms produced in response to the rare nontargets were averaged over a mean of 40 trials (ranging from 34-45 trials) for the first sequence and 38 trials (ranging from 24-45 trials) for the second sequence.

The waveforms (see figures 4.1a and 4.1b) showed a negative deflection at approximately 100 ms in all three stimulus conditions (the N100), followed by a

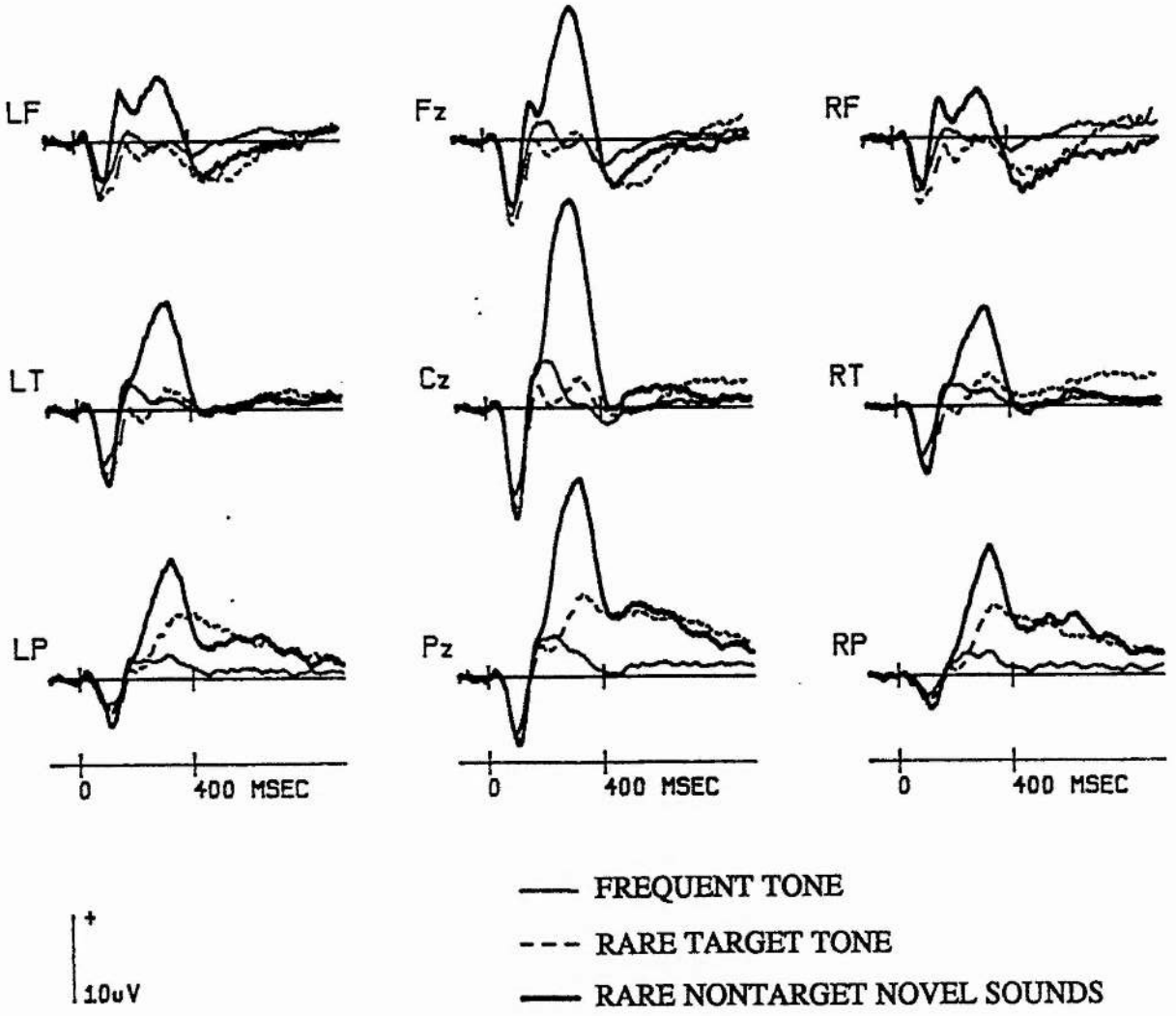


Figure 4.1a Waveforms, averaged over 12 subjects, for each condition of the first sequence of stimuli in experiment 1.

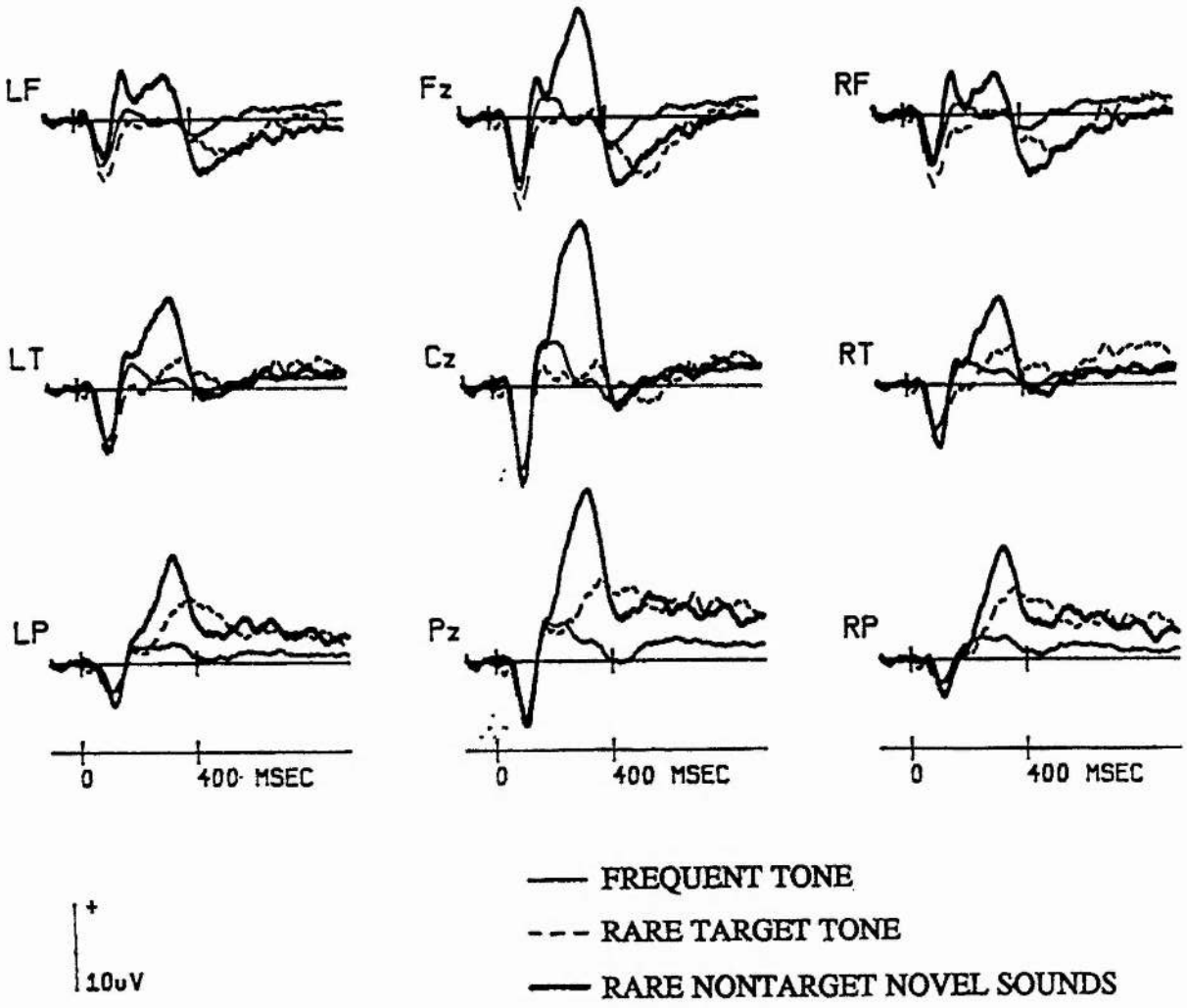


Figure 4.1b Waveforms, averaged over 12 subjects, for each condition of the second sequence of stimuli in experiment 1.

small positive deflection at approximately 170 ms which was most visible in response to the rare nontargets (labelled the P170). For the waveforms produced in response to the target and the rare nontarget stimuli, there then followed a larger positive deflection with a mean latency of 387 ms for the targets and 295 ms for the rare nontargets. These deflections were considered to be reflecting the contribution to the waveform of components of the P300 complex. These P300 deflections were followed by a sustained period of negativity at frontal sites and a period of positivity at posterior sites; this slow wave activity appears to be absent in the ERPs to the frequent stimuli. Analyses were carried out on the amplitudes and latencies of the N100, P170 and P300 deflections in the three conditions. As discussed in the general method, the mean amplitude of the area of waveform between 500 and 900 ms was used to investigate the negative and positive slow waves.

To determine the latency window within which the mean amplitude was to be measured, peak latency of the N100 was measured at Cz for all 3 conditions in all 12 subjects. The latency of the P170 was measured at Fz for all 3 conditions in individual subjects' waveforms. The latency used for determining the measurement window was obtained by calculating the mean peak latency over the three conditions. The P300 elicited by the target tones was labelled the P3b. Its latency was measured at Pz for 9 of the 12 subjects while for the other subjects it was not possible to determine the peak of the deflection. The P300 elicited by the novel sounds was labelled P3a. Its latency was measured at Fz, Cz and Pz in all 12 subjects. In this case the mean latency across the three sites was used to determine the measurement window.

Repeated measures ANOVAs were performed on mean amplitude measurements. 12*2*2*3*3 (subject*sequence*condition*chain*site) ANOVAs were performed for

both P3a and P3b to compare the amplitude of the peak with the amplitude of the corresponding latency region of the waveform elicited by the frequents. This design ANOVA was also used to compare P3a and P3b amplitudes before and after the data had been rescaled. 12*2*3*3*3 (subject*sequence*condition*chain*site) ANOVAs were performed on the N100, P170 and the 500-900 ms region of waveform (slow wave) before and after rescaling.

RESULTS

P3a

The centro-parietally distributed positive deflection elicited by the novel sounds can be seen in the grand averaged waveforms for the two sequences of stimuli in figures 4.1a and 4.1b. This deflection was found to have a mean latency of 285 ms (SD=22.5) and mean amplitude of 24.7 Microvolts within the region +-12 ms round the peak at Cz for the first stimulus sequence. This peak was also present in the waveform for the second sequence of stimuli with a mean peak latency of 296.3 ms (SD=26.9) and mean amplitude of 20.9 Microvolts within the region +-12 ms round the peak at Cz. The difference in latency between the two sequences was not statistically significant ($F(1,11)=0.151$, $P>0.05$).

The results of the ANOVA on the mean amplitude of the area of waveform measured +-12 ms round the peak for each subject are shown in Table 4.1. It can be seen that the amplitude of this deflection was significantly greater than that of the same area of ERP waveform produced in response to the frequent tones. This deflection will be labelled as the P3a.

Table 4.1. ANOVA summary table for analysis of the amplitude of the P3a elicited by the novel sounds and the same region of the waveform elicited by the frequent stimuli for the two testing stimulus sequences, before rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	1.92	0.194
Condition (CC)	1,11	114.47	0.000*
Chain (CH)	1.5,16.6	34.26	0.000*
Site (ST)	1.5,16.4	36.04	0.000*
SE*CC	1,11	2.42	0.149
SE*CH	1.4,15.9	2.89	0.098
SE*ST	1.5,16.2	0.61	0.504
CC*CH	1.9,20.4	64.90	0.000*
CC*ST	1.3,14.5	11.58	0.002*
CH*ST	2.1,23.6	1.81	0.184
SE*CC*CH	1.3,14.8	2.55	0.125
SE*CC*ST	1.2,12.8	0.45	0.540
SE*CH*ST	2.3,24.8	2.11	0.138
CC*CH*ST	2.6,28.7	3.98	0.021*
SE*CC*CH*ST	2.5,27.8	1.78	0.182

* indicates statistical significance at the 0.05 level or better

Table 4.2 Mean amplitude, from 12 subjects, of the P3a elicited by the novel sounds and the same area of waveform elicited by the frequent tones for each site, of each electrode chain (collapsed over sequence).

CONDITION	MIDLINE			LEFT			RIGHT		
	F	C	P	F	C	P	F	C	P
FREQUENT TONE	-0.2	1.4	3.1	-0.5	1.2	2.3	0.1	2.1	2.6
NOVEL SOUNDS	13.3	22.8	20.8	5.8	11.0	11.6	5.4	11.8	11.9

F=frontal sites C=central sites P=parietal sites

The results displayed in Table 4.1 show that there was no significant difference in the amplitude of the P3a peak elicited by stimuli in the two sequences and no significant interactions with sequence.

P3a amplitude differed significantly across the three chains of electrodes, this chain effect significantly interacted with condition. Newman-Keuls test of P3a amplitude across chain performed separately for the novel sounds and frequent tones showed that, whereas the novel sounds elicited a P300 which was larger in amplitude at midline than lateral sites, the same area of waveform elicited by the frequent stimuli showed no amplitude difference across electrode chains. The mean amplitudes are shown in Table 4.2.

A significant main effect of site was obtained which significantly interacted with condition. Newman-Keuls tests comparing amplitude of the P3a region of the waveform across site separately for the frequent stimuli and novel sounds showed that the P3a elicited by the novel sounds did not differ significantly in amplitude between parietal and central sites but was significantly larger at both these sites than at frontal sites, ie. had a centro-parietal maximum. The same area of waveform elicited by the frequent stimuli was significantly larger at parietal sites than at frontal sites but the amplitude at central and frontal and central and parietal sites did not differ. The mean amplitudes are shown in Table 4.2.

As shown in Table 4.1, a significant three way interaction was obtained between condition, chain and site. Newman Keuls testing showed this to be due to there being a larger difference in amplitude between midline and lateral sites, of the region of waveform +-12 ms round the P3a, at central sites than at frontal and

parietal sites in response to the novel sounds. This amplitude difference was not found for the frequent tones. This was because the P3a elicited by the novel sounds had a centro-parietal maximum at midline sites but a parietal maximum at lateral sites, whereas the same area of waveform elicited by the frequent tones had a parietal maximum at all electrode chains. The mean amplitudes are shown in Table 4.2.

P3b

A positive peak was observed in the waveform elicited by the target tones of the first stimulus sequence. This peak was found to have a mean latency of 382 ms (SD=53.3) and mean amplitude of 11.8 Microvolts within the region +-12 ms round the peak at Pz. The peak was also observed in the second stimulus sequence with a mean peak latency of 379 ms (SD=63.1) and mean amplitude of 12.2 Microvolts within the region +-12 ms round the peak at Pz.

The results of the ANOVA on the area of waveform measured +-12 ms round the peak for each subject are shown in Table 4.3. These results confirmed that the amplitude of the deflection was significantly greater than that of the same area of ERP waveform produced in response to the frequent tones. This deflection will be labelled as the P3b.

As can be seen in Table 4.3, the amplitude of the P3b region did not differ significantly between the two sequences and no significant interactions were seen with sequence.

Table 4.3. ANOVA summary table for analysis of the amplitude of the P3b elicited by the target tones and the same region of the waveform elicited by the frequent stimuli for the two testing stimulus sequences, before rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	0.71	0.415
Condition (CC)	1,11	34.73	0.000*
Chain (CH)	1.8,19.9	0.86	0.425
Site (ST)	1.3,14.4	68.79	0.000*
SE*CC	1,11	1.93	0.193
SE*CH	1.6,17.2	0.31	0.680
SE*ST	1.4,15.1	2.56	0.124
CC*CH	1.7,19.1	7.44	0.005*
CC*ST	1.2,13.0	24.16	0.000*
CH*ST	1.8,20.2	10.25	0.001*
SE*CC*CH	1.3,14.6	0.69	0.456
SE*CC*ST	1.2,13.7	0.20	0.717
SE*CH*ST	2.3,25.3	0.42	0.687
CC*CH*ST	2.6,28.8	1.57	0.222
SE*CC*CH*ST	2.2,23.7	1.02	0.382

* indicates statistical significance at the 0.05 level or better

Table 4.4 Mean amplitude, from 12 subjects, of the P3b elicited by the target tones and the same area of waveform elicited by the frequent tones for each site, of each electrode chain (collapsed over sequence).

CONDITION	MIDLINE			LEFT			RIGHT		
	F	C	P	F	C	P	F	C	P
FREQUENT TONE	-0.7	-0.1	1.7	-0.2	0.9	1.6	-0.2	1.3	1.7
TARGET TONES	1.0	4.3	12.0	-0.5	3.5	9.0	-0.1	5.1	9.6

F=frontal sites C=central sites P=parietal sites

A significant condition by chain interaction was obtained. Newman Keuls post hoc tests showed that in response to the target tones the P3b was significantly larger at midline than at left hemisphere sites but did not differ significantly between midline and right, and left and right hemisphere sites. In contrast, the same area of waveform in response to the frequent tones was significantly larger over lateral sites than over the midline. The mean amplitudes are given in Table 4.4.

A significant main effect of site was obtained which interacted significantly with condition. Newman Keuls tests, which compared the amplitude of the P300 region across site separately for targets and frequents, showed that the P3b in response to the targets increased in amplitude from frontal to parietal sites, whereas that in response to the frequents did not change in amplitude across site. A significant interaction was also found between chain and site. Newman Keuls tests showed that this was because the change in amplitude of the P3b region of the waveform between central sites and parietal sites was larger at the midline than at lateral sites and larger over the left than right hemisphere. In contrast, the change in amplitude of the P3b region of the waveform between frontal and central sites was larger at lateral sites than at the midline and larger over right than left hemisphere sites. The mean amplitudes are given in Table 4.4.

Comparison of P3a and P3b before rescaling

A significant difference in latency was found between the P300 deflection elicited in the two conditions ($F(1,11)=28.603$, $P<0.001$). The latency of the P3b was longer than that of the P3a. No significant interaction was found between condition and site, for both conditions the latency was shorter at central than at parietal sites producing a significant main effect of site ($F(1,11)=14.345$, $P<0.01$).

The results of the ANOVA comparing the amplitude of the P3a and the P3b are shown in Table 4.5. The results show significant main effects of condition, chain and site.

Significant interactions were obtained between condition and chain, and condition and site. These interactions will be discussed in relation to the analysis of the rescaled data. A significant three way interaction was produced between condition, chain and site which will also be discussed in relation to the analysis of the rescaled data.

Comparison of P3a and P3b after rescaling

Significant main effects of chain and site were obtained in the analysis of the rescaled data (see Table 4.5).

A significant interaction was obtained between condition and chain. Newman Keuls testing showed that this was due to the P3a elicited by the novel sounds being

Table 4.5. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli for the two testing stimulus sequences, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	0.58	0.462
Condition (CC)	1,11	53.70	0.000*
Chain (CH)	1.7,18.5	26.80	0.000*
Site (ST)	1.4,15.3	35.38	0.000*
SE*CC	1,11	4.06	0.069
SE*CH	1.3,14.4	2.10	0.168
SE*ST	1.7,18.4	0.53	0.566
CC*CH	1.6,17.9	56.20	0.000*
CC*ST	1.4,15.0	27.33	0.000*
CH*ST	1.9,21.0	1.19	0.323
SE*CC*CH	1.7,18.4	2.74	0.099
SE*CC*ST	1.1,12.2	0.55	0.488
SE*CH*ST	2.5,27.5	1.50	0.242
CC*CH*ST	2.9,32.3	8.31	0.000*
SE*CC*CH*ST	2.6,28.3	1.54	0.229

RESCALED AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	0.10	0.754
Condition (CC)	1,11	0.02	0.902
Chain (CH)	1.7,18.8	22.11	0.000*
Site (ST)	1.4,15.1	37.18	0.000*
SE*CC	1,11	0.00	0.959
SE*CH	1.3,14.5	0.10	0.828
SE*ST	1.8,19.4	0.24	0.758
CC*CH	1.5,16.8	40.83	0.000*
CC*ST	1.3,14.1	38.37	0.000*
CH*ST	1.9,20.5	1.20	0.319
SE*CC*CH	1.8,19.7	0.13	0.854
SE*CC*ST	1.1,11.7	0.87	0.375
SE*CH*ST	2.5,27.1	1.00	0.395
CC*CH*ST	2.8,30.6	10.72	0.000*
SE*CC*CH*ST	2.6,28.4	0.95	0.417

* indicates statistical significance at the 0.05 level or better

Figure 4.2 Graph illustrating the distribution, across electrode chain, of rescaled amplitude of the P300 deflection elicited by targets and rare nontargets in experiment 1 (collapsed over stimulus sequence and electrode site).

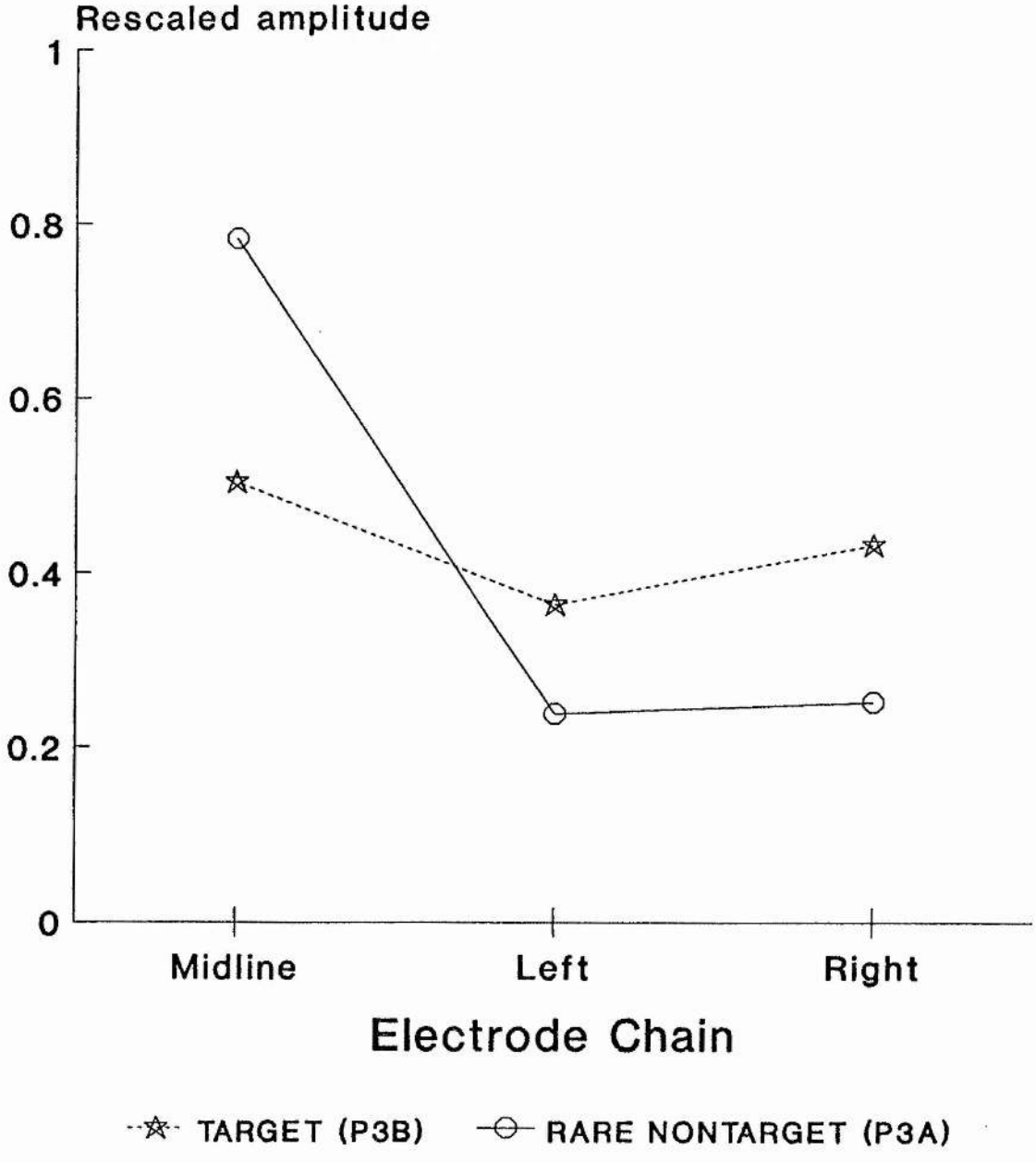


Figure 4.3 Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by targets and rare nontargets in experiment 1 (collapsed over stimulus sequence and electrode chain).

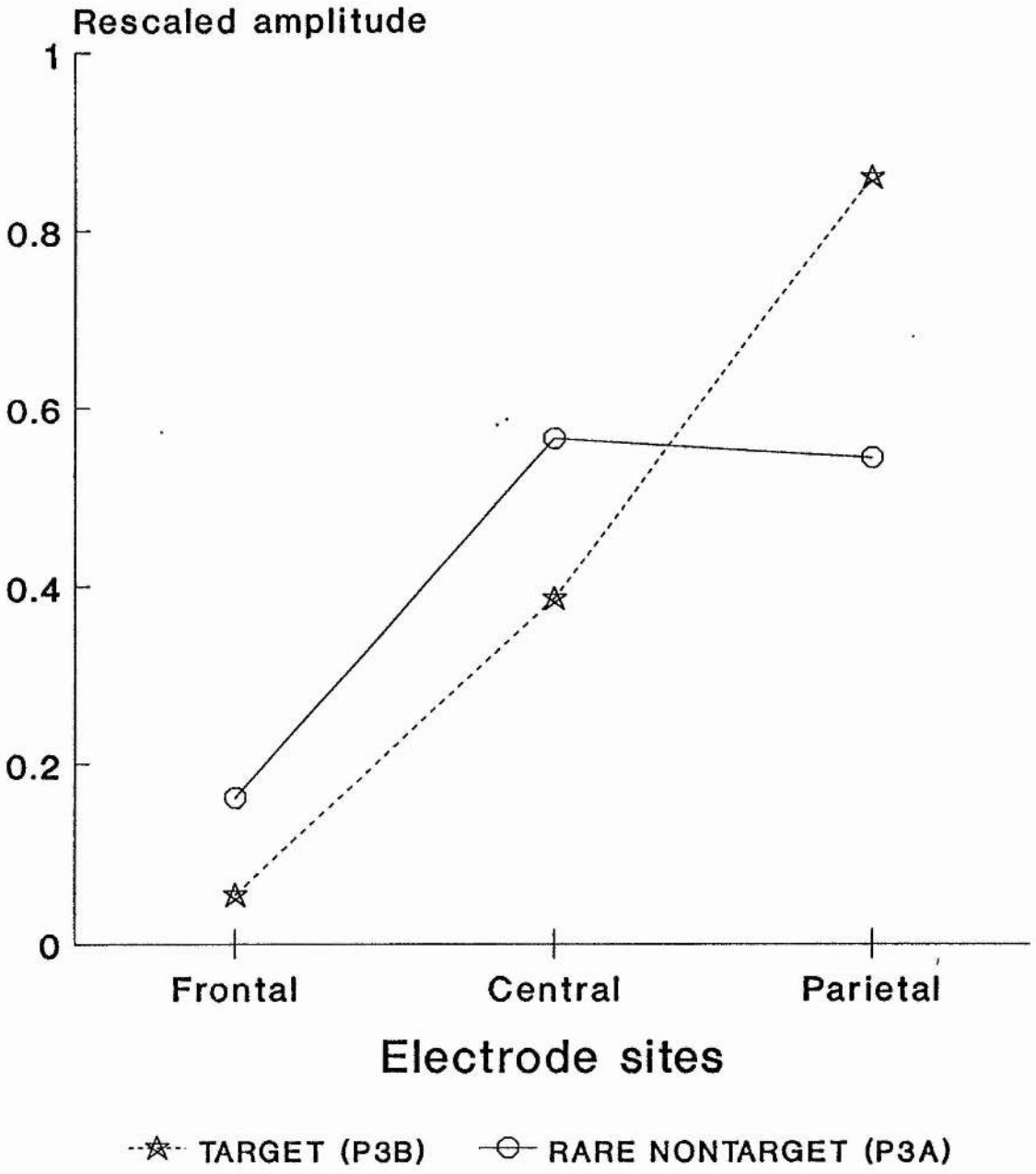


Table 4.6 Mean rescaled amplitude, from 12 subjects, of the P300 deflection elicited by the target tones and the novel sounds for each site, of each electrode chain (collapsed over sequence).

CONDITION	MIDLINE			LEFT			RIGHT		
	F	C	P	F	C	P	F	C	P
TARGET TONES	0.1	0.4	1.0	0.0	0.3	0.8	0.0	0.4	0.8
NOVEL SOUNDS	0.5	1.0	0.9	0.0	0.3	0.4	0.0	0.4	0.4

distributed more over midline sites than the P3b elicited by the targets (see figure 4.2).

A significant condition by site interaction was obtained. This was produced because the P3b elicited by the targets had a parietal maximum, whereas the P3a elicited by the novel sounds was distributed maximally over centro-parietal sites. The distribution of the two components across electrode site is illustrated in Figure 4.3.

A significant three way interaction between condition, chain and site was found in the analysis of the rescaled data. This was produced because the P3a elicited by the novel sounds showed a larger difference between the midline and lateral sites at the vertex than at frontal and parietal sites. This was because the P3a elicited by the novel sounds had a centro-parietal maximum at midline sites but a parietal maximum at lateral sites. Due to the parietal distribution of the P3b elicited by targets over both the midline and lateral sites, the differences between midline and lateral sites described above for the P3a were not present for the P3b. This can be seen from the mean rescaled amplitudes in Table 4.6.

N100 before rescaling

As can be seen in Table 4.7 of the appendix, no significant main effect of condition was found on the amplitude of the N100 deflection. There were no significant differences in N100 amplitude between the two stimulus sequences and no significant interactions with sequence.

N100 differed in amplitude across the three chains of electrodes. Newman Keuls tests comparing N100 amplitude across chain (collapsed over condition, site and

sequence) showed the N100 to be larger at midline than lateral sites. No significant interactions were found with chain.

A significant site effect was obtained which interacted significantly with condition. This interaction will be discussed in relation to the rescaled data.

N100 after rescaling

The results of the ANOVA are shown in Table 4.7 of the appendix. As for the analysis of the unrescaled data, the present analysis found no significant interactions with sequence.

A significant interaction was found between condition and site. Newman Keuls tests were performed to investigate the interaction by comparing N100 amplitude across site separately for each condition. The N100 elicited in response to the frequents and targets was significantly more negative at frontal and central sites than at parietal sites. The N100 elicited by the novel sounds was significantly more negative at central sites than at frontal and parietal sites which did not differ significantly. Therefore the interaction was produced because the waveform was significantly less negative at frontal sites in response to the novel sounds than in response to the targets and frequents. This interaction is illustrated in Figure 4.4.

A significant main effect of chain was obtained. Post Hoc tests showed that this was due to the N100 being significantly larger at midline than at lateral sites. As can be seen from Table 4.7 of the appendix, no significant interactions with chain were produced.

Figure 4.4 Graph illustrating the distribution, across site, of rescaled amplitude of the N100 deflection elicited by the three categories of stimuli in Experiment 1 (collapsed over stimulus sequence and electrode chain).

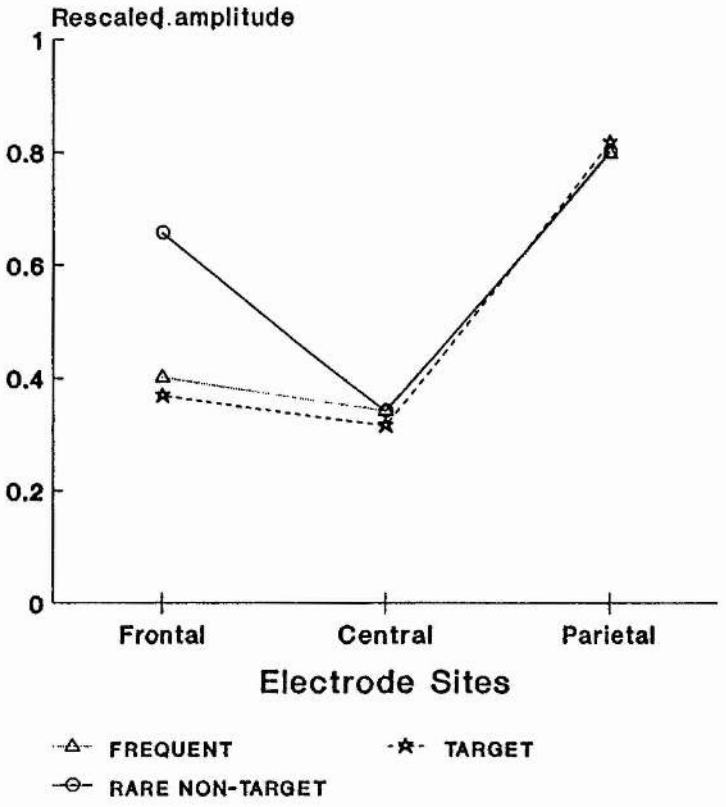


Table 4.9 Mean amplitude, from 12 subjects, of the P170 deflection elicited by frequent tones, target tones and novel sounds for each electrode site (collapsed over sequence and chain).

CONDITION	FRONTAL	CENTRAL	PARIETAL
FREQUENT TONE	-0.4	1.2	1.0
TARGET TONE	-2.5	-1.0	0.6
NOVEL SOUNDS	2.9	1.7	1.0

Table 4.10 Mean rescaled amplitude, from 12 subjects, of the P170 deflection elicited by the frequent tones, target tones and novel sounds for each site, of each electrode chain (collapsed over sequence).

CONDITION	MIDLINE			LEFT			RIGHT		
	F	C	P	F	C	P	F	C	P
FREQUENT TONES	0.1	1.0	0.9	0.0	0.3	0.3	0.1	0.4	0.3
TARGET TONES	0.1	0.7	1.0	0.1	0.2	9.5	0.0	0.3	0.6
NOVEL SOUNDS	0.6	0.6	0.8	1.0	0.4	0.1	1.0	0.5	0.0

P170 before rescaling

The results of the ANOVA are shown in Table 4.8. Inspection of the results shows that no significant main effects of sequence or condition were obtained and no significant interactions were produced with sequence.

Significant main effects of chain and site were obtained which interacted to produce a significant chain by site effect. This interaction will be discussed in relation to the rescaled data.

A significant interaction was found between condition and site. As can be seen from the mean amplitudes in Table 4.9, this was because the P170 elicited by the targets had its largest amplitude at parietal sites, the P170 elicited by the frequents was maximal at centro-parietal sites and that elicited by the novel sounds was of similar amplitude over all electrode sites.

P170 after rescaling

As shown in Table 4.8 of the appendix, the analysis of the rescaled data revealed significant main effects of chain and site.

The condition by site interaction reported above was not present in the analysis of the rescaled data.

A significant chain by site interaction was produced which post hoc testing showed was due to the P170 being distributed more over central and parietal sites at the

midline than at lateral sites. This can be seen in the mean rescaled amplitudes in Table 4.10.

Table 4.8 of the appendix shows a significant three way interaction between condition, chain and site. Inspection of the mean amplitudes in Table 4.10 showed that the frequent tones elicited a P170 with a central maximum for all three electrode chains. The P170 elicited by the targets had a parietal maximum for all three electrode chains whereas that elicited by the novel sounds had a central maximum at midline sites but a frontal maximum at lateral sites. The scalp distributions for the three conditions are shown in Figure 4.5.

500-900 ms region before rescaling

As can be seen from the ANOVA results in Table 4.11 of the appendix, the amplitude of the 500-900 ms region did not differ significantly between the two sequences of stimuli and no significant main effect of condition was found.

A significant site effect was obtained which interacted significantly with chain, this interaction will be discussed in relation to the analysis of the rescaled data. A significant condition by site interaction was obtained which did not remain in the analysis of the rescaled data. Post hoc testing showed that the amplitude of the 500-900 ms region of the waveform elicited by the frequent stimuli did not differ significantly across site, whereas the same area of waveform elicited by the targets and novel sounds was significantly more positive at parietal sites than at central sites and frontal sites and significantly more positive at central than at frontal sites. This can be seen in the mean amplitude measures in Table 4.12, which show that the 500-900 ms region of the waveform elicited by the targets and novel sounds was below

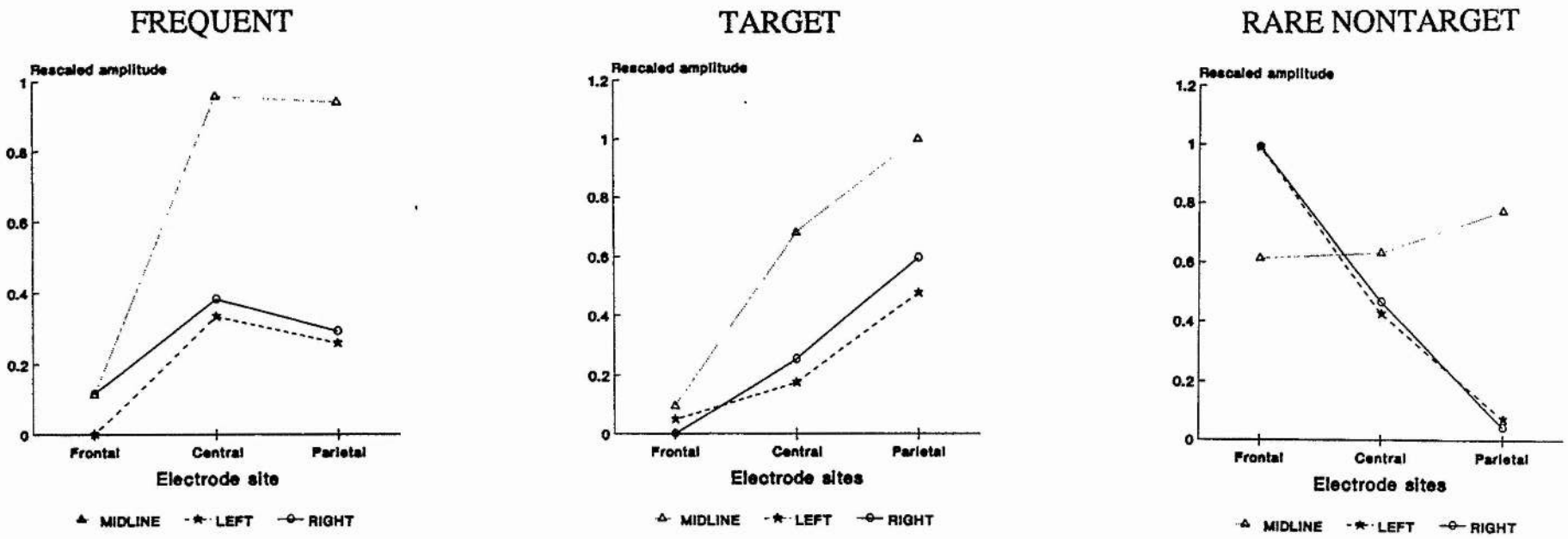


Figure 4.5 Graph illustrating the distribution of rescaled amplitude, over the sites of each electrode chain, for the P170 deflection elicited by the frequent, target and rare nontarget stimuli in experiment 1 (collapsed over stimulus sequence).

Table 4.12 Mean amplitude, from 12 subjects, of the 500-900 ms region of the waveforms elicited by frequent tones, target tones and novel sounds for each electrode site (collapsed over sequence and chain).

CONDITION	FRONTAL	CENTRAL	PARIETAL
FREQUENT TONE	0.7	0.9	1.1
TARGET TONE	-1.4	1.9	4.5
NOVEL SOUNDS	-2.0	1.1	4.4

Table 4.13 Mean rescaled amplitude, from 12 subjects, of the 500-900 ms region of the waveforms elicited by the frequent tones, target tones and novel sounds for each site, of each electrode chain (collapsed over sequence).

CONDITION	MIDLINE			LEFT			RIGHT		
	F	C	P	F	C	P	F	C	P
FREQUENT TONES	0.0	0.4	1.0	0.3	0.5	0.5	0.6	0.6	0.7
TARGET TONES	0.0	0.4	1.0	0.0	0.4	0.7	0.1	0.6	0.8
NOVEL SOUNDS	0.1	0.5	1.0	0.1	0.5	0.8	0.0	0.5	0.9

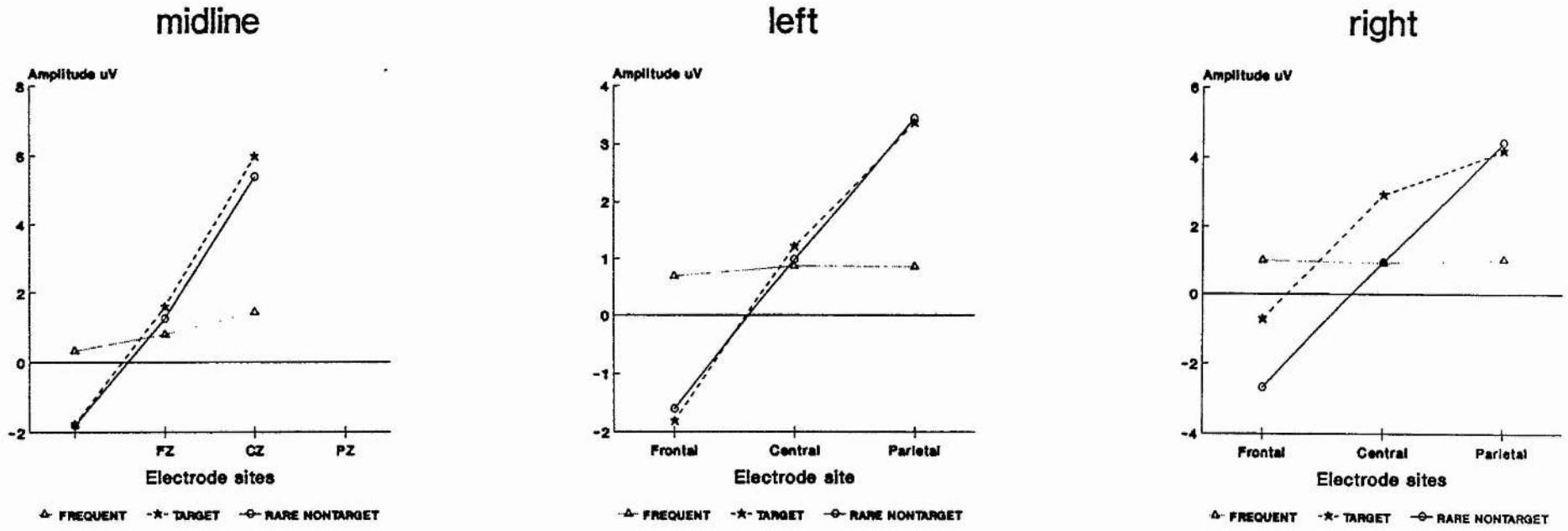


Figure 4.6 Graph illustrating the amplitude of the 500-900 ms region, at each electrode site, for each condition over the midline, left and right hemispheres in experiment 1 (collapsed over stimulus sequence).

the pre-stimulus baseline at frontal sites, that is, negative, but was positive at parietal sites. A significant condition by chain by site interaction was obtained (see figure 4.6) which again was not present in the analysis of the rescaled data. Newman Keuls post hoc tests showed that the interaction was produced because the change in amplitude of the 500-900 ms region of the waveform from central to parietal sites was larger at the midline than at lateral sites in response to the targets, larger at the midline than at left but not right sites in response to the novel sounds but did not differ between chains in response to the frequent stimuli. For all three conditions, the change in amplitude from frontal to central sites did not differ between electrode chains.

500-900 ms region after rescaling

As shown in Table 4.11 of the appendix, no significant interactions were found with sequence or with condition. The finding that no significant condition by site interaction was present suggests that there was no difference in distribution of the slow wave across sites in the three conditions. The mean rescaled amplitudes of the 500-900 ms region are given in Table 4.13.

A significant site effect was obtained which interacted significantly with chain. Newman Keuls tests comparing amplitude of the 500-900 ms region across chain for each site showed that at frontal and central sites no difference in amplitude was found between chains, whereas at parietal sites this area of the waveform was larger at midline than at lateral sites (see Table 4.13).

Table 4.14. Mean reaction time (ms) for the responses to the targets, mean number of hits, mean number of false alarms and the corresponding standard deviations, for the first and second run of the auditory oddball task of experiment 1.

	MEAN	SD
RUN 1		
Reaction time	475.0	76.3
Number of hits	43.4	4.3
Number of false alarms	0.4	0.5
RUN 2		
Reaction time	472.0	96.4
Number of hits	44.4	1.4
Number of false alarms	0.3	0.5

Behavioural data

Behavioural data is summarised in Table 4.14. No difference in mean reaction time to respond to the target tone ($t=0.11$, $P>0.05$) or the number of errors produced ($t=1.0$, $P>0.05$) was seen between the two sequences of stimuli.

Summary

A centro-parietally distributed positive deflection, with a mean latency of 285 ms, was obtained in response to rare nontarget novel sounds. A slightly later deflection with a parietal distribution was obtained in response to the target tones. These deflections were considered to reflect contributions to the waveform of the previously reported P3a and P3b components respectively. The P3a had a significantly larger amplitude and was distributed more over the midline than the P3b. A negative deflection, with a midline maximum, was obtained at approximately 100 ms in response to all stimuli in the task (the N100). The amplitude of this deflection did not differ between conditions but the distribution of amplitude across electrode site did differ. The N100 elicited by the novel sounds was distributed less over anterior sites than that elicited by the frequent and target tones. The N100 was followed by a positive deflection with a mean latency of 170 ms (P170). The distribution of this deflection differed between conditions. The P170 elicited by the frequents was distributed maximally over central sites, that elicited by the targets was distributed maximally over parietal sites and that elicited by the novel sounds was maximal at the vertex at the midline but had a frontal maximum at lateral sites. As this deflection was superimposed on the rising slope of the P300 deflection, the distribution of the P170 was affected by the distribution of the P300. Within the 500-900 ms region, which followed the P300 deflection, a

negative deflection was found at frontal sites and a positive deflection was found at posterior sites. Whereas the amplitude of this region of the waveform elicited by the frequents did not differ in amplitude across site, that elicited by the targets and novel sounds was significantly more positive at parietal sites than at central sites and more negative at frontal sites than at central sites.

DISCUSSION

P300

As reported in many previous studies, both categories of rare stimuli in the task elicited a positive deflection in the waveform between 250-450 ms which was not elicited by the frequently occurring stimuli. The area of waveform elicited by the frequent tones, which corresponded with the P300 latency region, did not differ significantly in amplitude across electrode sites. This finding supports previous reports that the P300 is elicited by stimuli with a low subjective probability and unpredictable time of presentation but not by frequently occurring stimuli. Naatanen's theory predicts that the frequent stimuli would not elicit a P300 since it is proposed that a neuronal trace of this stimulus would be passively formed in sensory memory. On subsequent presentations of the frequent stimulus a match would occur with the sensory memory trace. Since the elicitation of both the P3a and the P3b are, according to Naatanen's theory, dependent on the occurrence of a mismatch with the trace held in sensory memory, neither of these components would be expected to be elicited by the frequent stimuli. A P300 may be elicited by the frequent stimuli before a trace of the stimulus is formed, that is at the beginning of a sequence of experimental trials, or following the presentation of several rare stimuli

which would weaken the trace of the frequent stimulus. While a trace of the frequent stimulus is present, no P300 would be expected to be elicited. As this is true for most of the stimulus sequence, no P300 would be expected to be found in response to the frequent stimuli in the averaged waveform.

The P300 elicited by the rare auditory stimuli was found to be distributed differently across the scalp in response to the targets and the novel sounds, thus supporting the dissociation of the P300 complex reported previously by Knight (1984) and Knight et al. (1989). In the present study, the target tones elicited a P300 deflection with a parietal maximum of equal amplitude over all electrode chains. This was considered to be the previously reported P3b component. The novel sounds elicited a deflection in the P300 latency range which had a maximal amplitude at midline centro-parietal sites. The smaller P300 response to the novel sounds at lateral electrodes was distributed maximally over parietal sites. The P300 elicited by the novel sounds was considered to be that labelled the P3a by previous researchers. These previous studies, however, have reported the P3a component elicited by novel unexpected stimuli to have a fronto-central distribution rather than the centro-parietal distribution reported here (eg. Courchesne et al., 1975; Knight, 1984; Knight et al., 1989). The study by Yamaguchi and Knight (1991) is an exception to this and reports a P3a elicited in the somatosensory modality with a maximum amplitude at central sites. The scalp distribution of the P300 response to novel stimuli obtained in the present experiment differed from that reported previously. The finding that the distribution of the P300 deflection, across both site and chain, differed between the two conditions does suggest that the activity of at least partially different neural generators appear to be producing the P300 in response to the targets and novel sounds in the present experiment.

As discussed in Chapter 2 (General Method), the interpretation of ERP data is complicated by the fact that the peaks in the waveform often result from the overlap of various ERP components. In the present experiment, the possibility therefore exists that the P3b is produced by the same neural generator as the P3a but that it has a more posterior distribution because it is superimposed upon a larger late positivity than is produced in response to the novel sounds. An alternative suggestion is that the P3a may have a more posterior maximum, similar to that of the P3b, but that its amplitude is decreased at parietal sites by the overlap of a negative component. These explanations, however, are unlikely because no significant difference was found between conditions in the amplitude of the region of the waveform following the P3a and P3b (500-900 ms region) which may be expected to overlap these peaks. Further evidence for differing modulation of the P300 region of the waveform in the two conditions rather than differing contribution from overlapping earlier or later components will be provided in the experiments to be reported here.

The view taken here is that the different scalp distributions of the P300 produced in response to the target tones and the novel sounds in the present experiment were due to differential activation of neural generators by the two categories of rare stimuli and may reflect different psychological processes. It is possible that the P300 elicited by the novel sounds in the present experiment showed a centro-parietal rather than the previously reported fronto-central distribution because of the combination of a frontal P3a component and a, slightly later, more posteriorly generated P3b component which together produced a centrally maximal peak. The P3b contribution to this P300 deflection may have been produced because subjects employed a strategy in which the frequently occurring stimulus was ignored due to its predictability and lack of significance within the task, leaving a respond/do not respond decision to be made in response to the equally rare targets and novel sounds.

Although the deflection reported here may not be a "pure" P3a component, it will be referred to here as such to distinguish it from the parietally maximal P3b elicited by the targets.

The P3a and P3b showed no differences in amplitude between the two sequences. This suggests that there was no long term habituation of either component across subsequent presentations of the corresponding stimulus.

The P3a occurred at a significantly earlier latency than the P3b. This may suggest that less processing of the stimulus is required before the processes reflected by the P3a are elicited than for those reflected by the P3b.

N100

In the present experiment the N100 component showed no decrease in amplitude from the first to the second stimulus sequence. This suggests that no long term habituation of the N100 is maintained across a 30 second break,a length of time which allows recovery of refractory neurons. No significant difference in the amplitude of the N100 was found between the three conditions. This result was surprising because, as discussed in Chapter 1 (General Introduction), the N100 generating neurons (at least for component 1) are thought to become refractory upon repeated presentation of the same stimulus. Inspection of the waveforms in Figures 4.1a and 4.1b shows that the difference in amplitude between conditions is in the expected direction, with the amplitude of the N100 elicited by the targets and novel sounds being equal and larger than that elicited by the frequents. The dissociation of the N100 into a number of components was reviewed in the General Introduction. It is possible that the reason there is only a small difference in N100 amplitude

between the frequent and rare stimuli is that other components, whose generator neurons do not become refractory on repeated presentation of the stimulus, overlap the first component.

The N100 elicited by stimuli in all conditions had a midline maximum but, whereas that elicited by targets and frequent stimuli had a maximum amplitude at frontal/central sites, the N100 elicited by the novel sounds had a central maximum. There are two possible reasons for this effect. Firstly, the N100 recorded in the waveforms elicited by the frequent and target tones and the novel sounds could have been produced by different neuronal generators, ie. the N100 or combination of N100 components elicited by the tones and the novel sounds differed. This may be due to the very fast onset time or the complexity of the novel sounds compared with the tones. An alternative explanation for the effect is that the same fronto-centrally distributed N100 is being produced in response to the tones and the novel sounds but that in the case of the novel sounds there is overlap from a frontal positivity which reduces the amplitude of the N100 at frontal sites. The P170, which was found to have a larger contribution from frontal sites when elicited by the novels than when elicited by the tones may be onsetting during the N100 latency range and so decreasing the amplitude of this component at frontal sites for the novel sounds. In summary, although the fronto-central distribution of the N100 recorded here in response to the frequent and target tones is suggestive of the elicitation of component 1 identified by Naatanen and Picton (1987), it is not possible to determine the contribution of other negative components within this latency range. In addition, it is not certain whether the difference in scalp distribution of the N100 elicited by the tones and the novel sounds is due to a differential pattern of activation of N100 neuronal generators or to the overlap of a frontal positivity.

P170

The P170 was found to be larger in response to the novel sounds than in response to the frequent and target tones. This peak possibly results from the overlap of a P200 component elicited by all tones (Goodin et al., 1978) and a slightly earlier component dissociated from the P200 by Goodin et al. and labelled the P165. The P165 was found to be elicited by attended rare tones in a two stimulus oddball task. Goodin et al. (1978) observed the peak in the waveform resulting from the subtraction of the waveform elicited by the rare tones when they were ignored from that elicited by the same tones when they were actively attended. This procedure cancelled out the contribution of the overlapping P200 present in both waveforms. The differing distribution of the P170 in the three conditions probably reflects the differing contribution of the P200 and P165 between conditions. Inspection of the waveforms indicates that the P170 is often superimposed on the slope of the wave between the N100 and the P300 and so the scalp distribution of these components may influence the apparent scalp distribution of the P170. The functional significance of the P165 is not as yet known. Goodin et al. (1978) suggest that it may reflect early neuronal events related to processing of target stimuli, possibly involved in stimulus identification and classification or response selection. Inspection of the waveforms shows the P170 elicited by the targets and novel sounds to be more similar than that elicited by the frequents which, as both rare stimuli require a response, is consistent with this suggestion.

500-900 ms region

The region of the waveform between 500-900 ms showed no habituation from one sequence of stimuli to the next. No difference in scalp distribution was found

between the three experimental conditions. This suggests that the activity of the same neuronal generator is being recorded in response to all stimuli. The waveform within this region was of maximum negativity at frontal sites and maximum positivity at parietal sites. These results are consistent with previous reports of slow wave activity overlapping and following the P300. The first report of a slow wave which could be distinguished from other components of the P300 complex was that of Squires et al. (1975). In this study, rare low probability attended auditory stimuli elicited a slow wave with an onset of 180 ms and duration of between 700-1000 ms which was positive at Pz, of zero amplitude at Cz and negative at Fz. This finding was replicated by subsequent studies which required subjects to count auditory stimuli (McCarthy and Donchin, 1976; Duncan-Johnson and Donchin, 1977). These initial studies found that the conditions for the occurrence of the slow wave were very similar to those of the P3b. However, a number of studies have provided explicit evidence for the dissociation of the P3b and the slow wave. Roth et al. (1978) employing a go/no-go paradigm found that a larger slow wave but smaller P3b was associated with faster reaction times, with the reverse being true for slower reaction times. Ruchkin et al. (1980a) found that the amplitude of the slow wave increased as difficulty of detecting the stimulus increased, whereas the amplitude of the P3b decreased with detection difficulty. Kok and Looren de Jong (1980) found that previous exposure to visual stimuli which had to be remembered in the experimental task had no effect on the amplitude of the P3b but that a subsequent P4, which may be related to the slow wave discussed above, was larger in amplitude in response to unfamiliar stimuli. In the present experiment the 500-900 ms region of the waveform elicited by the target tones and novel sounds was found to be more negative at frontal sites and more positive at parietal sites than that elicited by the frequent stimuli; a finding consistent with reports that the slow wave is larger in response to low probability than in response to high probability stimuli. The results

of the present experiment found the 500-900 ms region to be equally large following the P3a elicited by the novel sounds as it was following the P3b elicited by the targets. This therefore provides further evidence in support of its independence from the P3b.

Picton and Stuss (1980) have suggested that the slow wave may result from the overlap of a frontal negative and posterior positive potential. This is supported by a number of studies which report that an experimental manipulation affects either the negative or positive part of the waveform more than the other (eg. Fitzgerald and Picton, 1981; Friedman et al., 1981; Naatanen et al., 1982). Loveless et al. (1987) show that even when the frontal negative shift and parietal positive shift are associated in the averaged data, investigation of the single trials reveal that large frontal negativities are often accompanied by small posterior positivities and vice versa.

In the results of the present experiment, the amplitude of the 500-900 ms region of the waveform was found to be distributed equally across the three electrode chains at frontal and central sites but to be distributed maximally over the midline at posterior sites. This suggests the possibility of the presence of two overlapping slow waves; a posteriorly generated slow wave with a midline maximum and a more anterior slow wave distributed with a broader distribution across electrode chain. This dissociation is also suggested by the finding that the difference in amplitude of the 500-900 ms region between the low probability and frequent stimuli is larger at posterior than at frontal sites. It has been suggested that the slow wave reflects further processing of the stimulus subsequent to that reflected by the P300. The latency of the deflection in the present experiment is consistent with this. The nature of the further processing following detection of the stimulus (which is

thought to be indexed by the P3b) may vary between experimental tasks. This may account for why some studies have reported phasic slow waves whereas others have reported tonic slow waves (Ruchkin and Sutton, 1983). Longer latency slow waves which differ in scalp distribution, polarity and onset latency have also been reported in relation to perceptual and conceptual processing.

Behavioural Data

As shown in Table 4.14 of the Results, subjects made very few errors in responding to the target tone, indicating that the subjects did not find the task too difficult. No practice effect was found between the two sequences of stimuli probably because performance was already at ceiling for the first sequence.

Summary

The present experiment has provided further evidence in support of a dissociation of the P300 complex elicited in an auditory oddball task. A parietally maximal P3b was elicited by the target tones, whereas a centro-parietally maximal P3a was elicited by the novel sounds. A negative deflection in the N100 latency region, a subsequent positivity with a latency of approximately 170 ms and slow wave following the P3a and P3b were observed in the waveforms. The elicitation of these components was consistent with findings of previous studies.

CHAPTER 5

EXPERIMENT 2: INVESTIGATING WHETHER THE P3A IS ELICITED WHEN ALL STIMULI IN AN ODDBALL PARADIGM ARE TONES OR ALL ARE NOVEL SOUNDS.

INTRODUCTION

The results of Experiment 1 confirmed the previously reported distinction between a parietally distributed P3b in response to rare target stimuli and a more anteriorly distributed P3a in response to rare novel stimuli which do not require a response. The present experiment and those which follow, investigate the conditions necessary for the elicitation of the centro-parietal P3a in order to gain some insight into its psychological significance.

The P3a elicited by the sounds in Experiment 1 could have occurred for a variety of reasons. The first possibility is that the P3a is elicited by all rare stimuli presented within a stimulus sequence which do not require a response. This proposal is not supported by the findings of Courchesne et al. (1975, 1977), who reported that easily recognisable rare nontarget visual stimuli produced a P3 with a parietal distribution. This suggests that being a rare nontarget may be necessary but is not sufficient to produce a P3a in the visual modality. It is not known whether this finding extends to the auditory modality.

The second possibility is that the P3a is produced because the novel sounds are physically very different from the tones or more complex than other stimuli in the sequence. The proposal that a physical deviation from other stimuli in the sequence

is sufficient for P3a elicitation does not appear to be supported by experimental findings in the visual modality. Courchesne et al. (1978) used a task in which target letter Bs, with a probability of 10%, had to be detected within a sequence of letter As which had a probability of 80%. The remaining 10% of the sequence consisted of nontargets thought to be of varying deviance from the other stimuli in the sequence. These were repetitions of the letter C, a random selection of the letters C-Z and a random selection of the numbers 0-23. In a second procedure, the frequent and target stimuli were the same as above but the nontargets were either letters C-Z, letters C-Z with a lower luminance than the other stimuli in the sequence or letters C-Z with a higher luminance than other stimuli in the sequence. It was found that a posteriorly distributed P300 was elicited in response to all recognisable rare nontarget visual stimuli. This suggests that physical deviation of the stimulus from the background is not sufficient for the elicitation of the P3a. The stimuli which deviated in luminance from the background stimuli produced a larger amplitude P3 than the other rare nontarget stimuli, which led the authors to argue that more deviant stimuli elicit larger amplitude P300s. The same effect of deviation from the background stimuli has been observed on the amplitude of the P3b elicited by target stimuli. Ford et al. (1976) presented subjects with a series of tones in which there was occasionally a tone of a different pitch from that of the background stimuli. The difference in pitch between the frequent and background stimuli was either 5%, 25% or 100%. The deviant tones elicited a P300 which increased in amplitude with increasing mismatch from the frequent stimuli. This occurred both while the subject was reading, and therefore should have been ignoring the tones, and while the subject was attending to the tones. However, the effect was larger in the attention condition. These findings therefore suggest that physical deviation may affect the generator processes of both components but is not involved in determining which neuronal processes are activated.

Courchesne et al. (1978) suggested that the P300 deflection elicited by visual targets and easily recognisable nontargets differed in scalp distribution from that elicited by unrecognisable visual stimuli because of the differential ease with which the events could be categorised. He suggested that easily categorised events would produce a parietally distributed P300 deflection and those which could not be categorised would produce a frontally distributed P300 deflection. In the Courchesne et al. (1978) study the frontal P300 in response to the novel unrecognisable stimuli decreased in amplitude at frontal sites and increased in amplitude at parietal sites with repetition of the novel stimuli. Courchesne suggested that this reflected the formation of categorisation rules. A slight posterior shift in distribution on subsequent presentations of the novel stimuli was also reported in the auditory modality (Knight, 1984).

The model of auditory processing proposed by Naatanen (1990) suggests that the P3a occurs as a consequence of a mismatch between a neuronal model of the frequently occurring stimulus which is passively formed in sensory memory and a representation of the presented stimulus. Detection of a mismatch causes an orienting of attention to the presented stimulus. The P3a is thought to reflect a process which is a precursor of or related to the orienting of attention. If the stimulus is a target, the mismatch with the trace of the frequent is detected and the central executive mechanisms accessed. The stimulus is identified as a target and both the processes underlying the generation of the P3b and those required to make a response are invoked. This suggests that whenever the stimulus mismatches the representation of the frequent stimulus sufficiently to cause the central executive mechanisms to be accessed and the stimulus is found not to require a response, a P3a

is obtained in the waveform. When a response is required the resulting P300 peak consists of overlapping P3a and P3b components.

In the present experiment subjects were presented with two stimulus sequences. In one sequence the frequent, target and rare nontarget stimuli were three different tones, in the other sequence the stimuli were three different novel sounds. The conditions, to which the stimuli within each sequence were assigned, were balanced across subjects (e.g. in the tone oddball task one subject may have a high tone as the frequent stimulus, another subject may have a medium tone as the frequent and a third subject may have a low tone as the frequent). Any differences in the ERP waveforms between conditions within a task would not be due therefore to the physical characteristics of the stimuli but would be due to the role of the stimuli in the experiment. All stimuli in a sequence were equally deviant, no one stimulus of a sequence 'stood out' from the others, so any difference in the ERP waveforms elicited by the stimuli could not be due to difference in deviance.

The present experiment allowed the investigation of two alternative hypotheses. The first was that, as proposed in the model of auditory processing of Naatanen (1990), if a rare nontarget stimulus mismatches the sensory memory representation of the physical features of the frequent stimulus, it would elicit a P3a. As discussed above, the results of the visual experiment of Courchesne et al. (1978) do not support this proposal since in that experiment the rare nontarget stimuli elicited a P300 deflection with a posterior maximum. However, it is possible that different processes are involved in auditory and visual processing. The first hypothesis therefore proposed that a P3a would be elicited by the rare nontarget stimuli in both the tone and novel sound oddball tasks.

The second hypothesis was that the P3a is elicited because of something intrinsic to the novel sounds and that the nature of the other stimuli in the task and the condition to which the novel sound is assigned are irrelevant. This hypothesis therefore proposed that a P3a would be elicited by all the novel sounds in the novel sound oddball task.

METHOD

Subjects

Twelve healthy subjects (mean age 21, range 19-25 yrs, 6 female) were tested. All were paid volunteers.

Design

Subjects were presented with two 300 trial stimulus sequences. One sequence consisted of a random mixing of a frequent tone (P=0.70), a target tone (P=0.15) and a rare nontarget tone (P=0.15). The tones were of 1000 Hz, 750 Hz and 500 Hz, allocated to condition in a balanced way across subjects. The other sequence consisted of the random mixing of a frequently occurring novel sound (P=0.70), a target novel sound (P=0.15) and a rare nontarget novel sound (P=0.15). Three different sounds were used and as for the tones were allocated to conditions in a balanced way across subjects. The order in which the two sequences were presented was balanced across subjects; six subjects completed the tone oddball first and six completed the novel sound oddball first. Prior to each experimental sequence

subjects were presented with a practice sequence of 15 stimuli. This sequence included 9 frequent, 3 target and 3 rare nontarget stimuli.

Procedure

For the tone oddball task subjects were told that a sequence consisting of high, medium and low tones would be presented through the headphones. Subjects were instructed to press the response button as quickly as possible, whilst avoiding errors, whenever they heard the tone which had been specified as the target and not to respond to the other stimuli. For the novel sound oddball task subjects were told that a sequence of three different sounds would be presented through the headphones. Subjects were instructed to press the response button as quickly as possible, whilst avoiding errors, as soon as they heard the sound which had been specified as the target. Responses were made with the preferred hand. Following successful completion of the practice trials each sequence of experimental trials was presented as three blocks of 100 trials with a 30 s break between each block.

DATA ANALYSIS

The grand average waveforms for the two tasks are shown in Figure 5.1a and 5.1b. These waveforms were obtained by averaging together the ERPs produced by the twelve subjects.

For the tone task, the waveform produced in response to the frequent stimuli was averaged over a mean of 164 trials (ranging from 103-184 trials), that in response to the target stimuli was averaged over a mean of 35 trials (ranging from 15-44 trials)

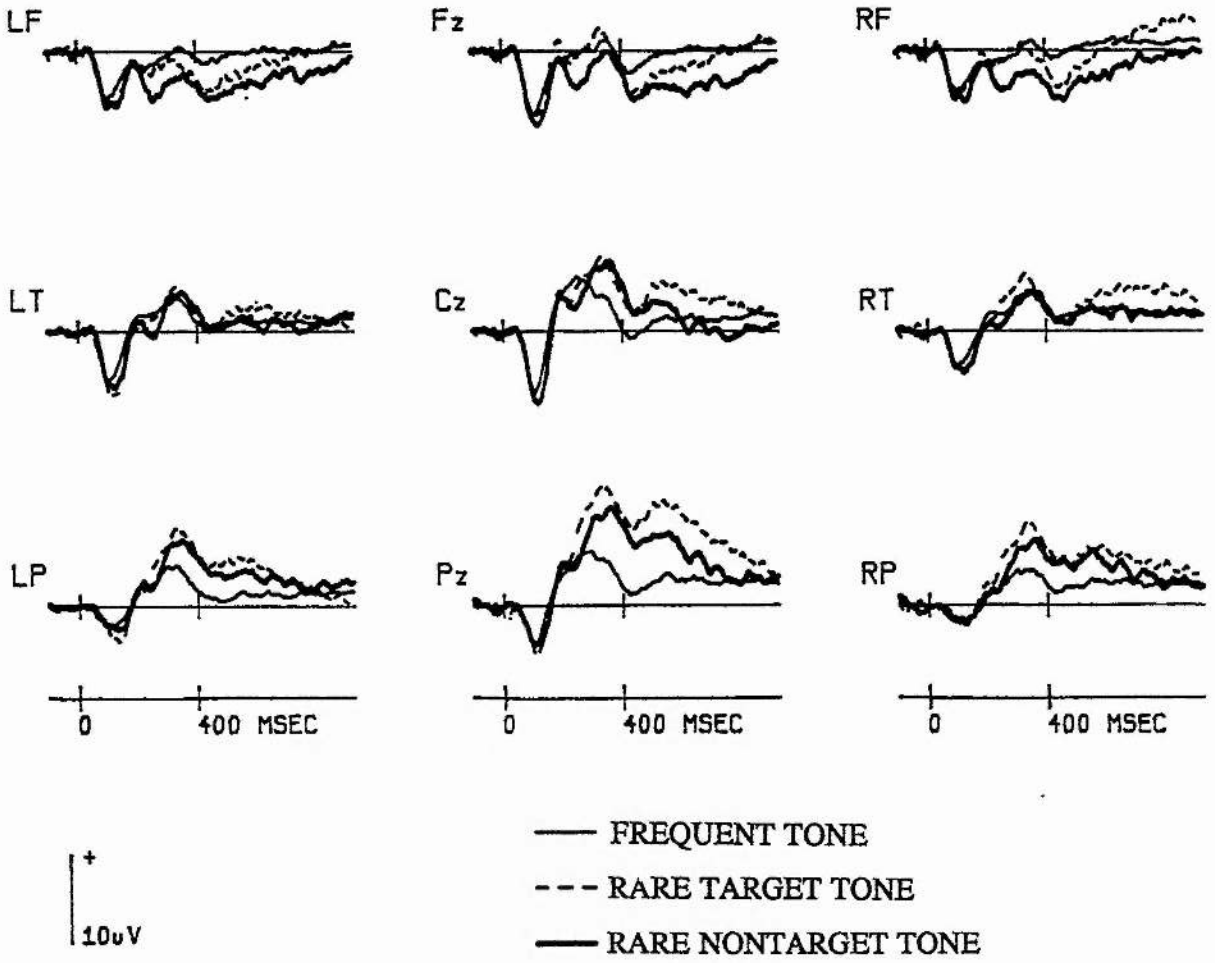


Figure 5.1a Waveforms averaged over 12 subjects for each condition in the tone oddball task of experiment 2.

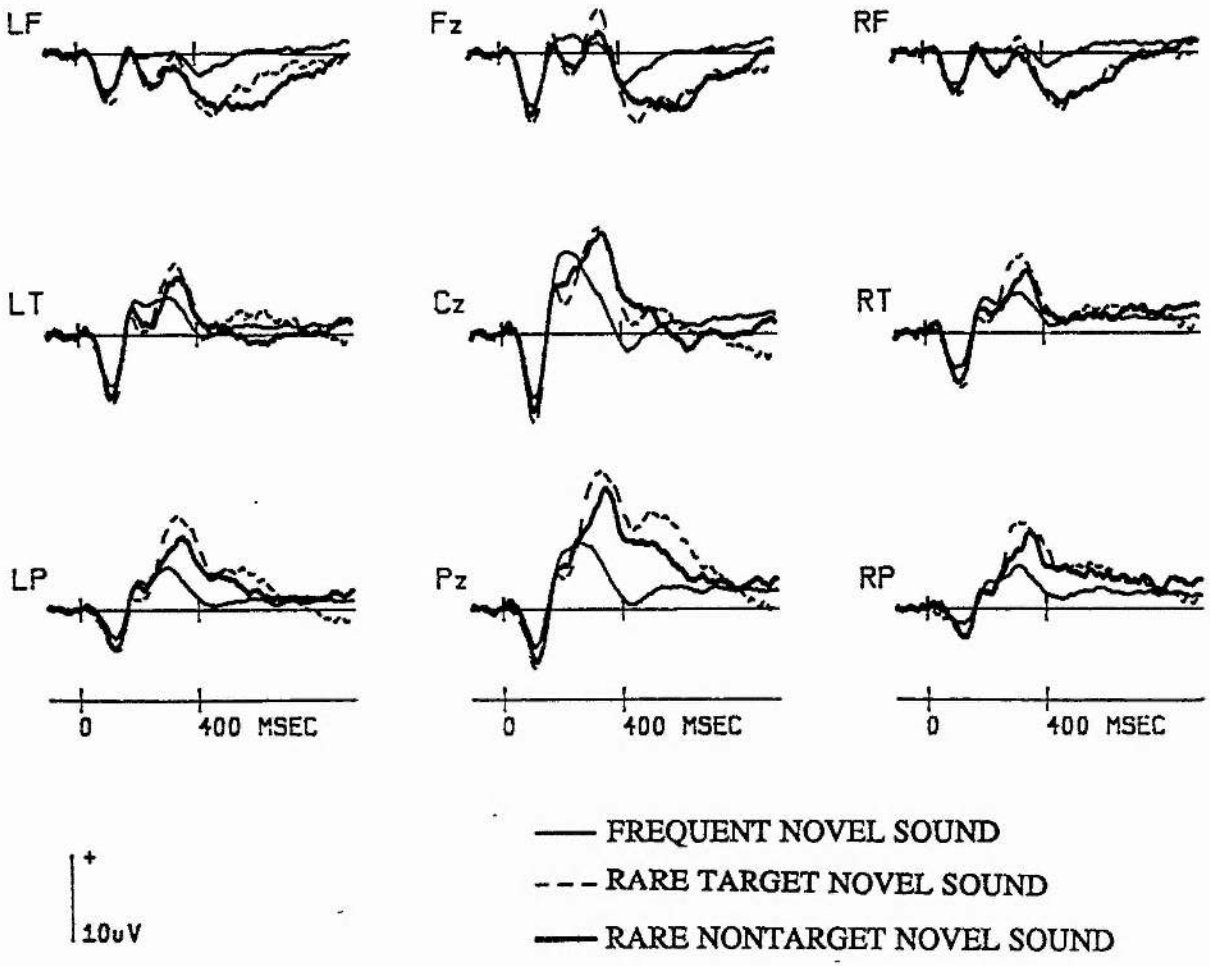


Figure 5.1b Waveforms averaged over 12 subjects for each condition in the novel sound oddball task of experiment 2.

and that in response to the rare nontarget stimuli was averaged over a mean of 34 trials (ranging from 24-44 trials). For the novel sound task, the waveform in response to the frequent stimuli was averaged over a mean of 172 trials (ranging from 140-200 trials), that in response to the target stimuli was averaged over a mean of 35 trials (ranging from 21-45 trials) and that in response to the rare nontargets was averaged over a mean of 38 trials (ranging from 29-43 trials).

As shown in Figures 5.1a and 5.1b, for both the tone and novel sound oddball task a negative peak was obtained at approximately 100 ms in all three conditions (referred to as N100 in Experiment 1). This was followed by a small positive deflection in the waveforms of the rare target and nontarget stimuli; this peak was most clearly visible at frontal sites (referred to as the P170 in Experiment 1). In the waveforms elicited by the two categories of rare stimuli the P170 was followed by a negative deflection, this will be referred to as the N200. A positive deflection, which was largest in amplitude at posterior sites, was subsequently seen in response to the rare targets and nontargets (the P300 deflection). This was followed by a sustained period of negativity at frontal sites and positivity at parietal sites which was not observed in response to the frequent stimuli.

As in the previous experiment, the latency of N100 was measured at Cz and that of P170 was measured at Fz for all three conditions for both the novel sound and tone oddball tasks. It was possible to obtain measurements of the three peaks for all 12 subjects. The mean latency of the peak over the three conditions was used to determine the latency window for each task. To determine the mean amplitude of the N200, the latency of the N200 deflection was measured in the grand average waveform elicited by the rare nontargets in both the novel sound and tone oddball task. The mean amplitude of the waveform +-12 ms round the N200 peak was

found for each of the three conditions, for each subject. The latency of P300 was measured at Pz in the waveforms elicited by the rare targets and rare nontargets of the two tasks. Measurements for each peak were made for all 12 subjects. Separate latency windows were determined in each task for the targets and rare nontargets. The latency region investigated in the waveform elicited by the frequent stimuli corresponded to that of the P300 peak with which it was being compared. The period of sustained negativity and positivity was investigated by performing analyses on the area of waveform within the 500-900 ms latency region.

Repeated measures ANOVAs were performed on the amplitude measurements for each component. A 12*2*2*3*3 (subject*sequence*condition*chain*site) ANOVA was performed comparing the amplitude of the P300 region of the waveform elicited by the frequent and rare target stimuli, the frequent and rare nontarget stimuli and the rare target and rare nontarget stimuli, of each task, before and after rescaling. 12*2*3*3*3 (subject*sequence*condition*chain*site) ANOVAs were performed on the amplitude of the N100, P170, N200 and 500-900 ms regions of the waveform before and after rescaling. Additionally, for the N200 the ANOVAs were repeated comparing the waveforms elicited by the targets and rare nontargets. This was because the N200 was only elicited by stimuli in these two conditions.

Between group, 2*12*2*3*3 (experiment*subject*condition*chain*site), ANOVAs were performed comparing the amplitude of the P300 elicited by the targets and rare nontargets in experiment 1 and the tone and novel sound oddball tasks of the present experiment before and after rescaling. Separate 2*12*3*3*3 (experiment*subject*condition*chain*site) ANOVAs were performed for the N100, P170 and 500-900 ms region comparing the amplitude of the deflection in

experiment 1 with that elicited by stimuli in the same conditions in the tone and novel sound tasks of the present experiment before and after rescaling.

RESULTS

P300

Inspection of the grand average waveforms of both tasks revealed a positive deflection with a posterior maximum in response to the rare targets and nontargets but not in response to the frequent stimuli. This was found to have a mean peak latency of 366 ms in response to the targets and 347 ms in response to the rare nontargets in the tone oddball task. The same positive deflection was found to have a mean peak latency of 331 ms in response to the targets and 338 ms in response to the rare nontargets in the novel sound oddball task. The ANOVA comparing the peak latencies of the two conditions in the two tasks showed no significant main effects of task ($F(1,11)=1.170$, $P>0.05$) or condition ($F(1,11)=0.379$, $P>0.05$) and no significant task by condition interaction ($F(1,11)=1.455$, $P>0.05$). The component will be referred to here as the P300 because although it has the same distribution as the P3b reported in the previous two experiments (see analysis of rescaled data) it can also be elicited by novel sounds.

P300 region for targets v frequents

As can be seen from Table 5.1, the results from the analysis comparing the amplitude of the P300 elicited by the targets with the equivalent region of waveform elicited by the frequent stimuli were as obtained for Experiment 1. This was true for

Table 5.1. ANOVA summary table for analysis of the amplitude of the P300 elicited by the target tones and the same region of the waveform elicited by the frequent stimuli for the two tasks, before rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	1.29	0.282
Condition (CC)	1,11	46.52	0.000*
Chain (CH)	1.7,19.2	21.80	0.000*
Site (ST)	1.3,14.4	40.36	0.000*
TA*CC	1,11	2.28	0.160
TA*CH	1.3,14.7	0.09	0.839
TA*ST	1.5,16.6	0.52	0.551
CC*CH	1.7,19.1	12.28	0.001*
CC*ST	1.3,14.3	26.01	0.000*
CH*ST	3.3,35.9	5.60	0.002*
TA*CC*CH	1.7,19.1	1.54	0.239
TA*CC*ST	1.6,17.3	0.60	0.522
TA*CH*ST	2.1,22.9	1.24	0.310
CC*CH*ST	2.5,27.1	2.59	0.084
TA*CC*CH*ST	2.8,31.2	1.26	0.305

* indicates statistical significance at the 0.05 level or better

Table 5.2. ANOVA summary table for analysis of the amplitude of the P300 elicited by the rare nontargets and the same region of the waveform elicited by the frequent stimuli for the two tasks, before rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	2.65	0.113
Condition (CC)	1,11	8.60	0.014*
Chain (CH)	1.7,18.8	21.09	0.000*
Site (ST)	1.5,16.4	68.42	0.000*
TA*CC	1,11	1.13	0.311
TA*CH	1.9,20.6	0.08	0.911
TA*ST	1.4,15.7	0.99	0.365
CC*CH	1.7,18.8	21.88	0.000*
CC*ST	1.2,12.9	40.97	0.000*
CH*ST	3.3,36.0	3.01	0.039*
TA*CC*CH	1.4,15.4	0.70	0.460
TA*CC*ST	1.6,17.9	0.25	0.734
TA*CH*ST	2.6,29.0	0.65	0.570
CC*CH*ST	2.8,31.3	3.55	0.027*
TA*CC*CH*ST	2.3,25.8	0.40	0.708

* indicates statistical significance at the 0.05 level or better

Table 5.3. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli for the two testing stimulus sequences, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	2.96	0.113
Condition (CC)	1,11	7.19	0.021*
Chain (CH)	1.8,19.8	29.85	0.000*
Site (ST)	1.2,13.4	60.74	0.000*
TA*CC	1,11	0.14	0.713
TA*CH	1.9,21.4	1.38	0.273
TA*ST	1.4,15.5	0.60	0.502
CC*CH	1.6,17.9	0.49	0.579
CC*ST	1.9,20.8	0.67	0.513
CH*ST	3.2,34.8	4.62	0.007*
TA*CC*CH	1.4,14.9	0.04	0.911
TA*CC*ST	1.5,16.9	0.49	0.570
TA*CH*ST	2.4,26.4	0.95	0.411
CC*CH*ST	1.9,20.8	2.36	0.122
TA*CC*CH*ST	2.7,30.2	1.11	0.357

RESCALED AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	0.06	0.810
Condition (CC)	1,11	0.08	0.787
Chain (CH)	1.8,19.8	29.91	0.000*
Site (ST)	1.2,13.4	61.10	0.000*
TA*CC	1,11	0.10	0.753
TA*CH	1.9,21.1	1.01	0.378
TA*ST	1.4,15.5	0.74	0.445
CC*CH	1.6,17.4	0.63	0.507
CC*ST	1.9,21.2	1.81	0.189
CH*ST	3.2,34.8	4.61	0.007*
TA*CC*CH	1.4,15.1	0.10	0.832
TA*CC*ST	1.6,17.2	0.12	0.840
TA*CH*ST	2.4,26.1	0.99	0.393
CC*CH*ST	1.9,20.6	2.21	0.138
TA*CC*CH*ST	2.7,29.8	1.16	0.340

* indicates statistical significance at the 0.05 level or better

both tasks. Post hoc testing showed that the interactions were obtained for the same reasons as in the first experiment and so will not be discussed here.

P300 region rare nontarget v frequent

As can be seen from Table 5.2, significant main effects of condition and chain were found which interacted to produce a significant condition by chain interaction as in Experiment 1.

A significant site effect was obtained which interacted significantly with condition. Newman Keuls post hoc testing showed this to be due to the P300 elicited by the rare nontarget stimuli increasing significantly in amplitude from frontal to parietal sites whereas the same region of the waveform elicited by the frequent stimuli was larger in amplitude at central and parietal sites than at frontal sites but showed no difference between the central and parietal sites.

A significant condition by chain by site interaction was obtained because the difference in amplitude of the P300 elicited at midline and lateral sites was larger for the rare nontargets than for the same region of waveform elicited by the frequent stimuli. For the rare nontargets, this amplitude difference was larger at central and parietal sites than at frontal sites.

P300 region target v rare nontarget before rescaling

As can be seen from Table 5.3, no significant effect of task was obtained. This suggests that the same effects were found for both the tones and novel sounds.

Table 5.3 shows a significant main effect of condition which was due to the P300 elicited by the target being larger in amplitude than that elicited by the rare nontarget. Significant main effects of chain and site were also found which will be discussed in relation to the rescaled data.

P300 region target v rare nontarget rescaled

As shown in Table 5.3, a significant effect of chain was found. The effect was obtained because the P300 was larger at midline sites than at both left and right hemisphere sites which did not differ from each other (Newman Keuls comparison of rescaled amplitude across chain collapsed over task, condition and site). Unlike Experiment 1, there was no significant condition by chain interaction.

Inspection of Table 5.3 shows a significant main effect of site. This was because amplitude of the P300 was larger at parietal sites than at central and frontal sites and that at central sites was larger than at frontal sites (Newman Keuls comparison of amplitude across site collapsed over task, condition and chain). Unlike experiment 1, no significant condition by site interaction was obtained. The scalp distributions of the P300s elicited by target and rare nontarget stimuli in the two tasks of the present experiment are shown in Figures 5.2a and 5.2b.

A significant chain by site interaction was obtained. For all sites the P300 was distributed more over the midline than laterally. This difference in distribution, however, is larger at posterior than frontal scalp sites in the comparison of midline with right hemisphere sites and is larger at central and parietal sites than frontal sites in the comparison of midline and left hemisphere sites.

Figure 5.2a Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by the target and rare nontarget in the tone oddball task of experiment 2.

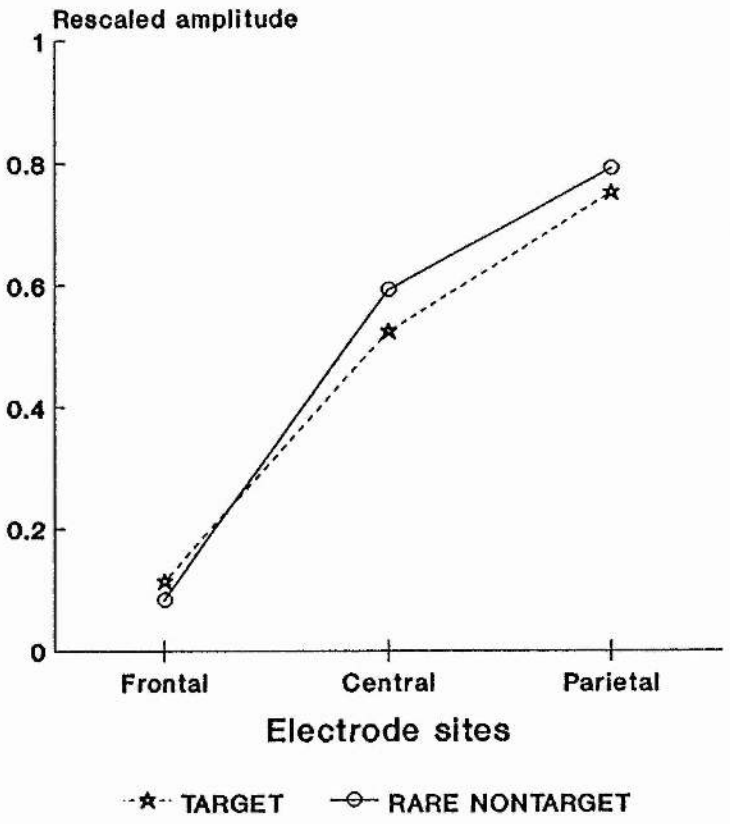
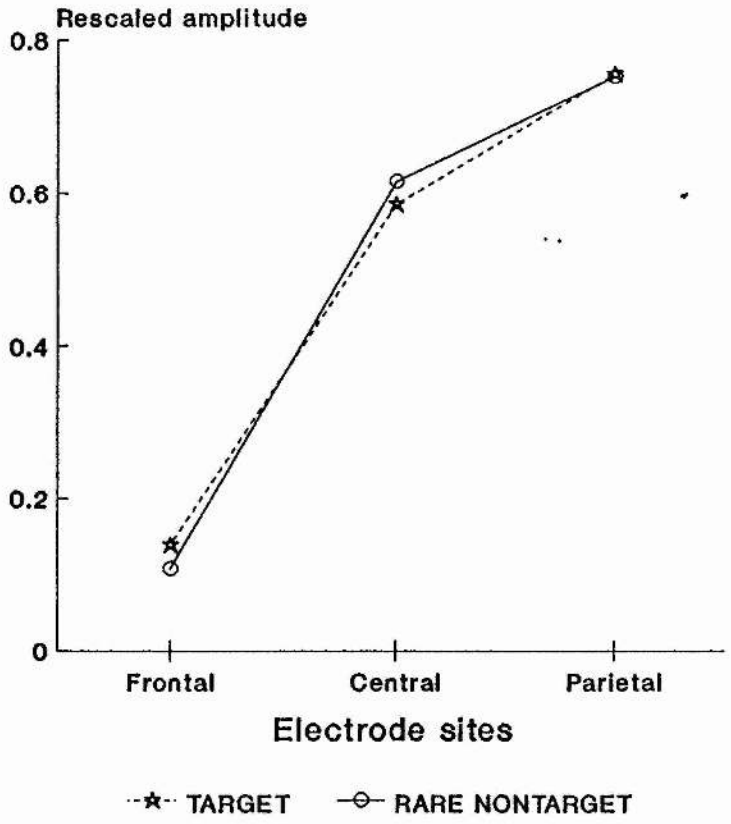


Figure 5.2b Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by the target and rare nontarget in the novel sound oddball task of experiment 2.



N100 before rescaling

The results of the ANOVA are given in Table 5.4 of appendix. It can be seen that a significant main effect of chain was obtained which interacted significantly with condition. The effect of chain was as obtained in experiment 1, that is being larger in amplitude over midline than lateral sites. According to the trend of the means which can be seen in Table 5.5, the condition by chain interaction was due to the larger difference between conditions over the midline than over the left hemisphere and larger difference over left than right hemisphere.

As shown in Table 5.4 of appendix, a significant main effect of site was obtained. Newman Keuls comparison of amplitude across site collapsed over task, condition and chain showed that amplitude was significantly smaller at parietal sites than at central and frontal sites which did not differ from each other. Interactions with site will be discussed in relation to the rescaled data.

N100 after rescaling

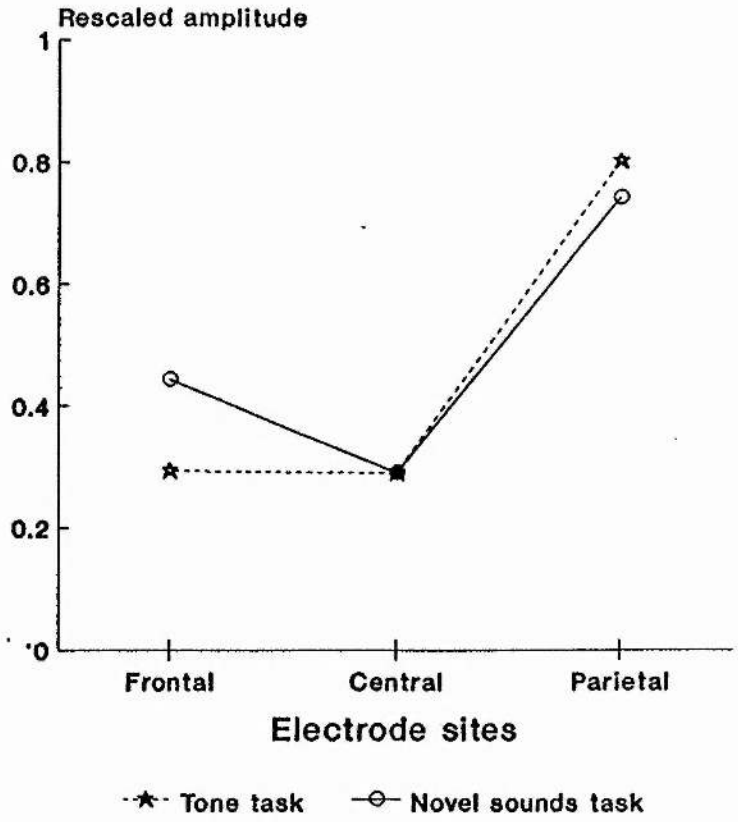
The results of the ANOVA are shown in Table 5.4 of the appendix. A significant chain effect was obtained which, as in Experiment 1, was due to the midline maximum of the N100.

Table 5.4 of the appendix shows a significant main effect of site which, unlike experiment 1, did not interact significantly with condition. The N100 therefore had the same distribution across site for all conditions. A significant task by site interaction was obtained. Newman Keuls tests showed that the difference in the

Table 5.5 Mean amplitude, from 12 subjects, of N100 deflection elicited by frequent, target and rare nontarget stimuli for each electrode chain (collapsed over task and electrode site)

CONDITION	MIDLINE	LEFT	RIGHT
FREQUENT TONE	-6.2	-4.5	-3.5
TARGET TONE	-7.9	-5.9	-4.3
NOVEL SOUNDS	-7.2	-5.3	-4.1

Figure 5.3 Graph illustrating the distribution, across site, of the N100 elicited by stimuli in the tone and novel sound oddball task (collapsed over condition).



amplitude of the N100 elicited by tones and novel sounds was larger at frontal than at central and parietal sites. The tones elicited an N100 with a fronto-central maximum, whereas that elicited by the novel sounds was less negative at frontal sites and therefore showed a central maximum. This is shown in Figure 5.3.

P170 before rescaling

As shown in Table 5.6 of the appendix, a significant chain effect was obtained. This was due to the amplitude of the P170 being larger at the midline than over left and right hemispheres which did not differ from each other (Newman Keuls comparison of amplitude across chain collapsed over task, condition and site).

Table 5.6 of the appendix shows a significant main effect of site. Newman Keuls test (comparing amplitude across site collapsed over task, condition and chain) showed that amplitude of the P170 was smaller at frontal sites than at central and parietal sites which did not differ from each other.

P170 after rescaling

The ANOVA results in Table 5.6 of appendix show a significant main effect of chain. As discussed above this was due to the midline maximum of the P170.

A significant main effect of site was obtained. As discussed above this was due to the centro-parietal maximum of the P170. A significant interaction was found between chain and site. This was because at frontal sites there were no significant differences between chains, whereas at central and parietal sites amplitude of the

P170 was larger at the midline than at lateral sites (Newman Keuls comparison of amplitude across chain for each site collapsed over condition and task).

N200 before rescaling

The results of the ANOVA comparing all three conditions are shown in Table 5.7 of the appendix and the results of that comparing the two rare conditions are shown in Table 5.8 of the appendix. It can be seen that there were no significant effects of task. This was surprising because inspection of the grand average waveforms shown in Figures 5.1a and 5.1b suggests that the N200 elicited by the rare nontargets is more negative than that elicited by the targets in the tone task but not the novel sound task.

No significant main effect of condition was found in either ANOVA. A significant condition by site interaction was obtained in the ANOVA comparing all three conditions. This interaction will be discussed in relation to the rescaled data.

A significant chain by site effect was obtained in both the ANOVA comparing three conditions and that comparing the two rare conditions. This interaction will be discussed in relation to the rescaled data.

N200 after rescaling

The results of the ANOVA comparing all three conditions are shown in Table 5.7 of the appendix and the results of that comparing the two rare conditions are given in Table 5.8 of the appendix. In the ANOVA comparing the two rare conditions, there

were no significant interactions with condition indicating that the N200 elicited by the targets and the rare nontargets were similar.

In the ANOVA comparing all three conditions a significant condition by chain interaction was obtained. Post hoc tests showed that the N200 elicited by the targets and the rare nontargets showed no significant difference in distribution across electrode chain. The distribution of the same area of the waveform elicited by the frequent stimuli differed more from those elicited by the rare stimuli over right hemisphere than left hemisphere and midline sites and more over left than midline sites. The region of the waveform elicited by the frequents was distributed less over lateral sites than that elicited by the rare stimuli.

The ANOVA comparing all three conditions showed a significant condition by site interaction. Post hoc testing showed that the N200 region of waveform, elicited by the two categories of rare stimuli, showed no differences in distribution across site. The same region in the waveforms elicited by the frequent stimuli, however, was distributed less over parietal sites than that of the rare stimuli but showed no differences at central and frontal sites.

As can be seen in Tables 5.7 and 5.8 of the appendix, a significant chain by site interaction was obtained in both ANOVAs. The N200 region was more positive at midline than at lateral sites, this difference was larger at parietal and central sites than at frontal sites.

500-900 ms region before rescaling

Inspection of the results of the ANOVA are shown in Table 5.9 of the appendix reveal very similar effects to those obtained in Experiment 1. In addition a significant interaction was obtained between task, condition and chain. This was because for the frequent stimuli and the rare nontargets the amplitude of the 500-900 ms region differed across chain in the same way for the two tasks, whereas that elicited by the targets had a larger amplitude at the midline in the tone than in the novel sound task.

500-900 ms region after rescaling

The results of the ANOVA on the rescaled 500-900 ms region data produced very similar results to those of experiment 1, as shown in Table 5.9 of the appendix.

Behavioural data

Behavioural results are summarised in Table 5.10. The number of targets correctly detected did not differ significantly between the two tasks ($t=-1.77$, $P>0.05$). The time taken to respond to the targets in the tone oddball task was significantly longer than that taken to respond to the target in the novel sound oddball task ($t=2.39$, $P<0.05$). A significantly greater number of false alarms were made in the tone oddball task than in the novel sound oddball task ($t=2.8$,$P<0.05$).

Table 5.10. Mean reaction time (ms) to respond to rare target stimuli, number of hits, number of false alarms and the corresponding standard deviations (SD) in the tone and novel sound auditory oddball tasks of experiment 2.

	MEAN	SD
TONE ODDBALL		
Reaction time	489.5	126.9
Number of hits	44.7	0.7
Number of false alarms	1.7	1.6
NOVEL SOUND ODDBALL		
Reaction time	452.3	123.2
Number of hits	45.0	0.0
Number of false alarms	0.4	0.5

Between Experiment Comparisons

P300 before rescaling

A between experiment ANOVA was carried out comparing the amplitude of the P300 region of the waveforms elicited by the target and rare nontarget stimuli of experiment 1 and the P300 region for the same conditions in the tone oddball task of the present experiment. A significant main effect of experiment was obtained ($F(1,22)=4.695, P<0.05$) because the amplitude of the P300 region, when collapsed over all within experiment factors, was larger in experiment 1 than in the tones oddball task; this was due to the larger amplitude of the P300 deflection elicited by the novel sounds in the former. A significant experiment by condition interaction was obtained ($F(1,22)=45.863$, $P<0.001$), this was significantly modified by chain producing an experiment by condition by chain interaction ($F(1.7,37.4)=30.017$, $P<0.001$) and site producing a significant experiment by condition by site interaction ($F(1.5,32.8)=8.339$, $P<0.005$). These interactions will be discussed in relation to the rescaled data.

An equivalent ANOVA was performed comparing the P300 region of waveform elicited in experiment 1 and the novel oddball task. No main effect of experiment was found ($F(1,22)=0.737$, $P>0.05$). A significant experiment by condition interaction was obtained ($F(1,22)=43.117$, $P<0.001$), which was significantly modified by chain producing a significant experiment by condition by chain interaction ($F(1.8,39.8)=22.889$, $P<0.001$) and by site producing a significant experiment by condition by site interaction ($F(1.5,33.4)=8.319$, $P<0.005$). These interactions will be discussed in relation to the rescaled data.

P300 after rescaling

ANOVAs were performed comparing the P300 region of the waveforms elicited in experiment 1 and the tone oddball task, and experiment 1 and the novel sound oddball task, after rescaling of the data. A significant experiment by condition by chain interaction was obtained ($F(1.6,36.3)=19.316$, $P<0.001$) in the comparison of experiment 1 and the tone oddball task and ($F(1.9,41.5)=13.657$, $P<0.001$) in the comparison of experiment 1 and the novel sound oddball task. Post hoc testing showed that in both cases, in the task from the present experiment, the P300 elicited by stimuli in the two conditions did not differ in distribution across electrode chain, both showing a midline maximum. In the task of experiment 1, the P300 elicited by the rare nontargets was distributed more over midline and less over lateral sites than that elicited by the targets, i.e. it had a strong midline maximum compared with the flatter distribution of that elicited by the targets.

A significant experiment by condition by site interaction was obtained ($F(1.4,31.4)=17.58$, $P<0.001$) in the comparison of experiment 1 and the tone oddball task and ($F(1.4,31.7)=18.294$, $P<0.001$) in the comparison of experiment 1 and the novel sound oddball task. This was because in both cases, in the oddball task from the present experiment no difference in scalp distribution was found between the two conditions, both having a parietal maximum. In the task of experiment 1, the P300 elicited by the rare nontarget stimuli was distributed more over central and frontal sites than that elicited by the targets and less over parietal sites than the targets.

N100 before rescaling

ANOVAs were performed comparing the amplitude of the N100 elicited by frequent, target and rare nontarget stimuli in experiment 1 and the tone oddball task, and in experiment 1 and the novel sound oddball task. A significant experiment by condition by site interaction was obtained ($F(2.5,55.6)=7.189$, $P=0.001$) in the experiment 1 versus tone oddball comparison and ($F(2.8,61.9)=4.752$, $P<0.01$) in the experiment 1 versus novel sound oddball comparison. These interactions will be discussed in relation to the rescaled data. No other interactions with experiment were significant.

N100 after rescaling

ANOVA comparing N100 elicited in experiment 1 and the tone oddball task, and in experiment 1 and the novel oddball task, after rescaling showed a significant experiment by condition by site interaction, ($F(2.6,57.5)=5.991$, $P<0.005$) and ($F(2.8,62.0)=3.437$, $P<0.05$) respectively. Post hoc testing showed that in the comparison between experiment 1 and the tone oddball task no significant difference between the two experiments was seen at any electrode site for both the frequent and target stimuli. For the rare nontarget condition the difference between the two experiments was larger at frontal sites than at central or parietal sites. For the comparison between experiment 1 and the novel sound oddball task, post hoc tests showed that in experiment 1 the N100 elicited by the frequent and target stimuli did not differ at any electrode site, in contrast, the difference in N100 between frequent and rare nontarget stimuli and between target and rare nontarget stimuli was larger at frontal than at central and parietal sites. In the novel sound oddball task no difference in N100 was found between the frequent and target

stimuli or target and rare nontarget stimuli at any electrode site, the difference in N100 between frequent and rare nontarget stimuli differed significantly between frontal and parietal sites.

P170 before rescaling

ANOVAs were performed comparing the P170 elicited by frequent, target and rare nontarget stimuli in experiment 1 and the tone oddball task and in experiment 1 and the novel sound oddball task. Significant interactions were found between experiment and chain ($F(1.5,32.2)=3.867$, $P<0.05$) for the comparison between experiment 1 and the tone oddball task and ($F(1.8,39.0)=5.164$, $P<0.05$) for the comparison between experiment 1 and the novel sound oddball task. A significant experiment by site interaction was obtained ($F(1.5,33.5)=5.895$, $P<0.05$) for the comparison with the tone oddball task and ($F(1.7,36.9)=4.47$, $P<0.05$) for the comparison with the novel oddball task. A significant experiment by condition by site interaction was obtained ($F(2.1,45.9)=7.927$, $P=0.001$) in the experiment 1 versus tone oddball and ($F(2.4,53.5)=4.269$, $P<0.05$) in the experiment 1 versus novel sound oddball. This interaction will be discussed in relation to the rescaled data. A significant experiment by chain by site interaction was obtained ($F(3.1,68.8)=3.119$, $P<0.05$) in the experiment 1 versus novel sound oddball comparison which will be discussed in relation to the rescaled data. This interaction was not found to be significant in the comparison between experiment 1 and the tone oddball task.

P170 after rescaling

ANOVAs were performed comparing the P170 elicited in experiment 1 and the tone oddball task and experiment 1 and the novel sound oddball task, after the data had been rescaled. A significant experiment by condition by site interaction was obtained ($F(1.9,42.3)=11.99$, $P<0.001$) for the comparison with the tone oddball task and ($F(2.2,48.5)=8.523$, $P<0.001$) for the comparison with the novel sound oddball task. Post hoc tests showed that in both cases this was because the P170 elicited by the frequent and target stimuli did not differ between the two experiments at any electrode site, a central maximum/parietal maximum being obtained in both experiments, whereas the P170 elicited by the rare nontarget stimuli had a frontal maximum in experiment 1 but a centro-parietal maximum in experiment 2. A significant experiment by chain by site interaction was obtained ($F(2.8,61.5)=3.714$, $P<0.05$) for the comparison with the tone oddball task, ($F(3.0,66.6)=3.512$, $P<0.05$) for the comparison with the novel sound oddball task. Post hoc tests showed that for both tasks the difference in P170 at the midline between the two experiments was larger at central than parietal or frontal sites because in experiment 1 a parietal maximum was obtained but in the present experiment a central maximum was obtained. Over the left and right hemispheres there was a larger difference in P170 over frontal sites than over central and parietal sites which did not differ. In experiment 1 the P170 was equally distributed across frontal, temporal and parietal sites but in the present experiment the P170 had a temporal-parietal maximum and was not found at frontal lateral sites.

500-900 ms region

ANOVAs comparing 500-900 ms region of waveform of experiment 1 with that of the tone and novel oddball tasks of experiment 2 showed no significant difference between experiments and no significant interactions with experiment.

Summary of Results

A P300 was evoked by the target and rare nontarget stimuli in both the tone and novel sound oddball tasks. No amplitude or latency differences were found between tasks. The amplitude of the P300 to the targets was significantly larger than that to the rare nontargets. P300 in response to stimuli from both conditions had a midline parietal maximum. N100 was evoked by stimuli in all three conditions and in both the tone and novel sound oddball task. No differences between condition or task were obtained. N100 amplitude was found to be significantly larger at midline than lateral sites and significantly larger at left than right hemisphere sites. N100 was distributed maximally over frontal and central sites. P170 with a midline centro-parietal distribution showed no differences between task or condition. The pre-stimulus baseline to peak amplitude of the N200 elicited by the two categories of rare stimuli showed a maximum positivity at parietal sites. The same region of waveform elicited by the frequent stimuli was found not to be as positive over parietal sites as that elicited by the two categories of rare stimuli. The distribution of the pre-stimulus baseline to peak amplitude of the N200 is affected by the superimposition of this deflection on the P300 for the rare stimuli which makes its investigation difficult. The 500-900 ms region of the waveform showed no significant difference between task or condition. Amplitude of the 500-900 ms region was more positive over right hemisphere than left hemisphere sites but amplitude at the midline did not differ significantly from that over either

hemisphere. At the midline, amplitude of the 500-900 ms region was found to be maximal at parietal sites, whereas at right hemisphere sites a centro-parietal maximum was obtained and at left hemisphere sites no significant differences were found between sites.

DISCUSSION

P300

The target and rare nontarget stimuli, in both the tone and novel sound oddball task, produced P300 deflections which did not differ significantly in scalp distribution or amplitude. The between experiment comparison showed that the P300 elicited by the rare stimuli in both the tone and novel sound oddball task had the same scalp distribution as that elicited by the targets in Experiment 1, i.e. a parietal maximum. The only difference between the P3b of Experiment 1 and the P300 obtained in the present experiment was that it was distributed slightly more over the midline in the present experiment and in the case of the novel sound oddball task was larger in amplitude.

These results suggest that a P3a is not elicited by all rare nontarget stimuli. This finding suggests that a P3b can be elicited by stimuli which do not require a specific response, e.g. silent counting or a motor response such as pressing a button.

The findings also suggest that the P3a is not elicited by all complex or 'novel' sounds since if this were the case a P3a would have been elicited by all stimuli in the novel oddball task. The findings also suggest that the P3a is not elicited by 'novel'

sounds when they are rare nontargets irrespective of the nature of the other stimuli in the experiment. If the P3a was elicited by all infrequent 'novel' sounds which did not require a response, a P3a would be elicited by the rare nontargets in the novel sound oddball task. As this was not the case it is suggested that some sort of comparison process between the novel sounds and the other stimuli in the task is necessary in order to elicit the P3a.

The sounds in the novel oddball task elicited larger amplitude P300s than the stimuli in the tones oddball task. The amplitude of these P300s elicited by the complex 'novel' sounds was not, however, as large as that elicited by the 'novel' sounds in experiment 1 where the other stimuli in the sequence were tones. This suggests that part of the effect of the increased amplitude of the P300 in response to more deviant stimuli may be due to something intrinsic to the sounds, although deviation from the other stimuli in the task also has an effect.

It appears that ease of categorisation cannot account for the elicitation of the P3a. The novel sounds as individual stimuli were no more difficult to recognise and therefore categorise in the first experiment than in the novel oddball task of the present experiment. Despite this similarity, the rare nontarget novel sounds in the present experiment elicited a P3b, whereas the rare nontarget novel sounds in experiment 1 elicited a P3a. It is possible that the other stimuli in the sequence may affect the ease with which the stimuli in a particular condition can be categorised.

The results of the present experiment do not support the proposals of Naatanen (1990). Naatanen suggests that a mismatch would occur between the presented stimulus and the passively formed representation of the frequent stimulus held in sensory memory, which would produce a subsequent P3a in the waveform if the

stimulus does not require a response. It may be, however, that the features extracted in the formation of the passive neuronal trace are shared by the stimuli within the sequences in the present experiment, whereas in the first experiment the features of the novel sound and those represented in the neuronal trace may have differed sufficiently to produce a mismatch and P3a. It has been suggested by Naatanen (in press) that a threshold has to be overcome in order to trigger processing reflected by the P3a. It is possible therefore, that in the present experiment the mismatch is not sufficient to overcome the threshold.

It is possible that in order to elicit a P3a, the rare nontarget has to be from a different category of sound from the other stimuli in the sequence, which makes it stand out and capture attention. So it may be that a mismatch of category rather than a mismatch in terms of physical features is required for P3a elicitation. Renault et al. (1989) presented faces which were either familiar or unfamiliar, with the unfamiliar faces occurring with a lower probability. The subject in the experiment was a patient suffering from prosopagnosia who could not recognise familiar faces. A P3a was elicited by familiar but unrecognised faces and a P3b elicited by recognised faces. When the familiar and unfamiliar faces occurred with equal probability, the P300 deflection was of equal amplitude in each condition. The experiment shows that the individual faces are being categorised as either familiar or unfamiliar and the P300 is a response to the category and is influenced by the probability of the category rather than to the individual stimuli. In the study of Kutas et al. (1977) subjects were presented in one condition with a sequence of a single frequently occurring male name (0.80) and a single occasionally occurring female name (0.20), in another condition a sequence of several male (0.80) and several female names (0.20) was presented. Subjects were instructed to respond to the less frequent female names. A large amplitude P3b was obtained in response to the targets in

both conditions. Johnson and Donchin (1980) presented subjects with three stimuli of equal probability one of which had to be responded to. The P300s obtained suggested that the two nontarget stimuli were being treated as a single category with a probability twice that of the individual stimuli. These experiments show that stimuli in the oddball task are categorised and the subsequent P300 dependent on the probability of the category. Although Naatanen (1990) has suggested that the P3a reflects an earlier process which appears to occur prior to stimulus categorisation, a possible interpretation of the results presented here is that more than a physical mismatch may be necessary in order to elicit the P3a.

Another possibility for the difference in the distribution of the P300 elicited by rare nontarget stimuli in Experiment 1 and the present experiment is that the subjects are employing different strategies in the two experiments. In experiment 1 the most efficient strategy for performing the task would be to form a representation of the target, wait for this to occur and ignore the other stimuli in the sequence. The P3b would reflect further processing following target detection and the P3a possibly processes related to orienting of attention because the novel sounds are so "attention getting" that they can not be ignored. In the present experiment, as the two rare stimuli are more similar than in the first experiment, the most efficient strategy may be to wait until a frequent stimulus does not occur and then make a go/nogo judgement in response to the rare stimulus. In this case although only one rare stimulus requires a specific motor response (the target), the rare nontarget requires the inhibition of a response. Both categories of rare stimuli may therefore elicit a P3b. Previous studies, however, have reported that nogo stimuli elicit a centro-parietal P300 (e.g. Tueting and Sutton, 1976; Hillyard et al., 1976; Pfefferbaum et al., 1985; Jodo and Inoue, 1990) which questions the latter interpretation of the results.

N100

The main result to emerge from the analysis of the N100 component is that, within task, no differences in distribution were seen between conditions. There was, however, a difference in distribution of the N100 elicited by the stimuli in the tone and the novel oddball task. The N100 elicited by the novel sounds was less negative at frontal sites than that elicited by the tones, i.e. it had a central maximum rather than a frontal/central maximum. It therefore appears that novel sounds, irrespective of the condition which they occupy in the task or the other stimuli in the sequence, elicit an N100 which is less negative at frontal sites than that elicited by tones. This suggests that the distribution of the N100 or the combination of overlapping negative components in this latency region are dependent more on the physical nature of the stimulus than on the psychological variables active in the task. This is consistent with previous findings for the N100.

P170

The frontal maximal P170 elicited in response to novel sounds (rare nontargets) in experiment 1 was not found in response to the rare nontargets in the tone and novel sound oddball task. In the present experiment the P170 did not differ in scalp distribution between conditions and in all conditions showed a maximum amplitude at central and parietal sites. These findings suggest that the P170 is more dependent on the psychological variables in the experiment than on the physical characteristics of the eliciting stimulus. If the frontal maximum P170 elicited in Experiment 1 was elicited because the stimuli were novel (complex) sounds, it would have been elicited by all the stimuli in the novel sound oddball task. Being a rare nontarget

also is insufficient to elicit a frontally maximal P170 since neither the rare nontarget stimulus of the tone task nor that in the novel sound oddball task elicited a P170 which differed in distribution from that elicited by the other stimuli in the sequence. The frontally maximal P170 appears to be elicited by stimuli which do not require a response but which differ from other stimuli in the sequence possibly because they are from a different category of sounds or because they stand out and so capture attention. It is therefore probable that the P170 is related to the detection of a mismatch or orienting of attention, i.e. similar kinds of processes proposed by Naatanen (1990) to be related to the P3a. It is possible that the P170 in response to the rare nontargets in experiment 1 has a frontal maximum as opposed to the more posterior maximum in the present experiment because in the former it is superimposed on a more anterior P3 component onsetting within the P170 latency range and that this affects its apparent scalp distribution. One point against this argument is that the P170 elicited in experiment 1 is equally large at midline and lateral frontal sites, whereas the P3a on which it may be superimposed has a midline maximum, and so would only be expected to influence the apparent scalp distribution of the P170 at midline sites.

One interesting dissociation was that, whereas the P170 elicited by novel sounds was found to have a frontal maximum in Experiment 1 but not in the present experiment, the N100 elicited by the novel sounds was found to be less negative at frontal sites than that elicited by the tones in both experiments. This means that the proposal in experiment 1, that the less negative N100 at frontal sites could be due to the overlap of a frontal P170 onsetting within the N100 latency range, appears to be unlikely. The difference between conditions in the distribution of the N100 must be due to the differing combination of negative components within this latency region.

N200

As discussed in Chapter 1 (General Introduction), the N200 region would be expected to encompass the MMN and the N2b in the waveforms elicited by rare stimuli in the attended oddball task. Both components are thought to be elicited as a result of a mismatch between a trace of the frequently occurring stimulus, held in sensory memory, and the features of the presented stimulus (Naatanen, 1990). In the stimulus sequences used in the present experiment no difference in the mismatch would be expected between the frequent stimuli and the targets and rare nontarget stimuli and therefore no differences would be expected between the two rare conditions in the N200 region. Inspection of the waveforms shows that within the N200 region the frequent stimuli elicited a positive deflection, whereas both categories of rare stimuli elicited a negative deflection. No difference in the amplitude of the N200 region, from the pre-stimulus baseline, was found between the two rare conditions. The amplitude measurement used here investigated how positive or negative the peak of the N200 was with respect to the pre-stimulus baseline rather than the actual "size" of the N200. The amplitude above pre-stimulus baseline of the N200 peak was, therefore, probably influenced by the P300 component, on which it was superimposed. The influence of the P300 peak on the amplitude measurement of this region was further suggested by the finding that the scalp distribution of the N200 elicited by the two categories of rare stimuli did not differ, both showed the N200 region to be more positive, with respect to the pre-stimulus baseline, over parietal sites. The N200 region of the waveforms elicited by both categories of rare stimuli were also more positive over midline electrodes than over lateral sites. These scalp distributions are very similar to those described for the P300. The N200 region in the waveforms elicited by the frequent stimuli were found to have a different scalp distribution to those of the rare stimuli. Due to

problems measuring the N200 in individual subjects, the latency window for mean amplitude measurement was determined from the grand average waveform. It is possible that the latency of the N200 varied between subjects and did not correspond with that in the grand average for all subjects. This means that apparent differences between the N200 region in the grand average waveforms elicited by the rare stimuli may not have been significant because the latency window may have missed the N200 peak in some of the subjects. The results of the present experiment showed no significant differences between tasks, indicating that the same effects were found in this region whether the stimuli were tones or novel sounds. In summary, inspection of the waveforms for both the tone and novel sound task showed a negative deflection, following the P170 and superimposed on the slope of the P300, in response to the two categories of rare stimuli. This negative deflection was probably composed of the MMN and N2b. Although it was not possible to measure the absolute size of the N200 deflection, baseline to peak measurements gave an idea of whether the peak was behaving in the same way in the two conditions. No significant differences were found between the two conditions.

500-900 ms region

No differences were found in the 500-900 ms region of the waveform between the present experiment and experiment 1. The absence of a difference between experiments suggests that the processes reflected by this region of the waveform occur later, after the stimulus has been identified. The slow waves within the 500-900 ms region appear not to depend on the physical characteristics of the stimulus and processes related to or directly resulting from stimulus identification, but appear to be more dependent on the role of the stimulus in the task.

Behavioural data

The behavioural data shows that the subjects responded to the targets with the same speed as in Experiment 1 which shows that the stimuli were no more difficult to discriminate in the present task than in Experiment 1. The number of correctly detected targets is at ceiling and did not differ between the two tasks, indicating that the subjects found both tasks easy. The reaction times to respond to targets was found to be significantly longer in the tone than the novel sound oddball tasks indicating that subjects found it harder to detect the target in the tone oddball task. The number of false alarms was also significantly larger in the tone oddball task than the novel oddball task. It maybe that the targets and rare nontargets in the tone oddball task may have been more easily confused than in the novel sound oddball task. It may be difficult for the subject to remember whether the tone they hear is, for example, the lowest tone in the sequence or whether there is a tone lower than that. This would not occur for the sounds as these are distinct and do not occur along a continuum of pitch.

Summary

In summary, both the targets and rare nontargets of the tone and novel sound oddball tasks were found to elicit a parietally distributed P300 deflection. This finding suggests a number of things concerning the P3a. Firstly, it suggests that the P3a is not being elicited because of the physical characteristics of the novel sounds and is not elicited by rare nontarget novel sounds irrespective of the nature of the other stimuli in the sequence. It suggests that the existence of a mismatch between the features of the frequent stimulus and those of the rare nontarget stimulus is not sufficient to elicit the P3a. The findings could be interpreted by suggesting that the

mismatch with the representation of the frequent stimuli needs to overcome a threshold before the attentional switch signalling the P3a is triggered (Naatanen, in press). Other potential explanations of these results include the possible need for the novel sound to be from a different category of sound from the other stimuli in the sequence or be qualitatively different from the other stimuli or the possibility that a different strategy is being used in the present experiment compared with that used in experiment 1.

CHAPTER 6

EXPERIMENT 3: INVESTIGATING WHETHER THE P3A IS ELICITED BY TARGET NOVEL SOUNDS

INTRODUCTION

The results of the two preceding experiments suggest that the centro-parietally distributed P3a, elicited by rare non-target novel sounds, is produced by the overlap of posterior and more anteriorly distributed activity. The generator producing the more anteriorly distributed activity is thought to be activated by the detection of a mismatch between the presented stimulus and a neuronal model of the sensory features of the frequently occurring stimulus. Its activity is thought to be related to the orienting of attention (Naatanen, 1990). The novel sounds, when presented among tones as in Experiment 1, appear to be sufficiently different from the frequent stimuli to activate this process, whereas the rare tones in the first experiment and the rare stimuli of Experiment 2 were not sufficiently different from the frequent to activate the process or to activate it to the same extent as the novel sounds of experiment 1.

The activation of the generator producing posterior activity (for brevity I will refer to this as the posterior generator) is thought to be related to the processing of task relevant stimuli which require a response. This processing is thought to be related to the updating of context to aid processing of, and response to, the stimulus when it is subsequently presented (Donchin and Coles, 1988). It could be assumed that in a one channel, three stimulus, oddball task such as that used in the experiments

reported in this thesis both categories of rare stimuli gain access to attentional processing. Once they have been discriminated by attentional processing both categories of rare stimuli would require a 'response' and so would be expected to activate the posterior generator. On detection of the targets, a button press response is required, whereas the rare nontarget stimuli require an inhibition of this response. The task is therefore one in which the target is a go stimulus and the nontarget a no-go stimulus each occurring with the same probability. Simson et al. (1977b) reported a study in which both go and no-go stimuli of a go/no-go task both produced a posteriorly distributed P300 suggesting that both categories of stimuli were activating the posterior generator. In the Simson et al. (1977b) study subjects were presented with two stimuli, 1 s apart, and were required to respond to the second stimulus if it differed from the first but to withhold a response if they were the same. Both auditory and visual stimuli were used. The go stimuli were found to elicit a parietally maximal P300, whereas a centro-parietal P300 was elicited by the no-go stimuli. The distribution of the P300 elicited by the no-go stimuli was thought to be due to the influence of a CNV between the first and second stimulus. When the amplitude of the P300 to the no-go stimuli was measured against the baseline preceding the first stimulus, the P300 was found to have a parietal maximum. These findings suggest that the same process is being activated by targets and rare nontargets which is consistent with the parietally maximal P300 obtained in response to both categories of rare stimuli in experiment 2. It is suggested that the anterior shift in response to the novel sounds in experiment 1 is due to the activation of an additional process because of the nature of the rare nontarget stimuli and their relation to other stimuli in the sequence.

The present experiment tests the above interpretation of the results of Experiment 1. Subjects were presented with one of the stimulus sequences from Experiment 1 and

instructed to press a button whenever a novel sound was presented and do nothing in response to the rare tones. As in Experiment 1, the novel sounds occurred with a low probability. It is therefore predicted that the automatic comparison process with the sensory features of the frequent stimulus held in the neuronal trace will occur, resulting in the detection of a mismatch and therefore an anterior contribution to the P300 waveform. As the novel sounds require a motor response, a posterior contribution to the waveform would also be predicted. It is therefore proposed that a centro-parietally distributed P300 will be elicited by the target novel sounds.

A number of studies (Tueting and Sutton, 1976; Hillyard et al., 1976; Pfefferbaum et al., 1985; Jodo and Inoue, 1990), however, have reported topographic differences between the P300s elicited by the go and no-go stimuli. In the Pfefferbaum et al. (1985) study, for example, visual stimuli, either words or symbols, were presented indicating that the subject should respond or wait. A parietally maximal P300 was elicited by the go stimuli and a centro-parietally maximal P300 was elicited by the no-go stimuli. This suggests that all go stimuli, that is stimuli requiring a button press response, activate a generator which produces a parietally maximal P300. In contrast, no-go stimuli activate a different generator or combination of generators which produces a centro-parietally distributed P300. It is therefore possible that instead of the centro-parietal maximum P300 being produced by the overlap of earlier activity resulting from detection of a mismatch, it may have been produced because the novel sounds activated a no-go or combination of no-go generators. Jodo and Inoue (1990) also report a difference in scalp topography between the P300s elicited by go and no-go stimuli. Subjects were presented with a 200 trial go/no-go session once per day for six days. The P300 elicited by the no-go stimuli had a more anterior distribution than that elicited by the go stimuli. The P300 elicited by no-go stimuli was later in latency for the initial sessions but by session

six was earlier in latency than that elicited by the go stimuli. Reaction time decreased over the sessions but no change in latency was found in the P300 elicited by the go stimuli. The results of these go/no-go experiments suggest an alternative hypothesis for the present experiment that the novel sounds, when targets, will elicit a P300 with a parietal maximum. The results of the experiments reported so far in this thesis do not appear to be consistent with this alternative hypothesis. In Experiment 1, the P3a elicited by the rare nontarget novel sounds was of earlier latency than the P3b elicited by the target tones (the go stimuli) which is inconsistent with the latency findings reported by Jodo and Inuoe (1990) for the P300 elicited by no-go stimuli. The latency of the P3a is more consistent with the suggestion that the centro-parietal maximum of the P3a is due to the contribution to the deflection of overlapping earlier activity. In Experiment 2, the rare non-target stimuli were found to elicit a parietally maximal P300 which would be inconsistent with the proposal that activation of a no-go generator(s) produces the centro-parietal P300, if subjects are treating the situation as a go/no-go task.

To summarise, the two alternative hypotheses tested in the present experiment are as follows. If the centro-parietal P300 elicited by the novel sounds in Experiment 1 was produced by the overlap of activity of a posterior generator, activated by stimuli requiring a response, and a generator producing a more anteriorly distributed deflection, activated by detection of a mismatch with the trace held in sensory memory, a P300 with the same scalp distribution would be predicted in response to the novel sounds when their presentation required a motor response. If, however, the centro-parietal distribution of the P3a obtained in Experiment 1 was produced because the novel sounds were no-go stimuli, a parietally maximal P300 would be predicted to occur in the present experiment as the novel sounds (targets) are now go stimuli.

METHOD

Subjects

Twelve healthy subjects were tested (mean age 23, range 19-36, 4 female). All were paid volunteers.

Design

Subjects were presented with one sequence of 300 stimuli consisting of the random mixing of a frequent high tone (P=0.70), a low tone (P=0.15) and different novel sounds each occurring a maximum of two times (P=0.15). The sequence of stimuli was exactly the same as one of the sequences used in Experiment 1. In contrast to Experiment 1, where the rare tones were the targets, in the present experiment the novel sounds were designated the targets. Prior to the presentation of the experimental sequence, subjects were presented with a practice sequence of 15 stimuli. This sequence included 9 frequent tones, 3 rare tones and 3 novel sounds requiring a response.

Procedure

The stimulus sequence was presented to subjects through headphones. The subjects were told that they would hear a sequence of sounds consisting mainly of high tones which were mixed with occasional low tones and other sounds which were similar to environmental noises. Subjects were instructed to press the response button

whenever they heard one of these other sounds. Responses were to be as fast as possible but with a minimal number of errors and were made with the preferred hand. Following successful completion of the practice trials the sequence of experimental trials was presented as three blocks of 100 trials with a 30 s break between each block.

DATA ANALYSIS

The grand average waveform is shown in Figure 6.1. This was obtained by averaging together the ERPs produced by the twelve subjects.

The waveforms produced in response to the frequent tones were averaged over a mean of 165 trials (range 116-197), those in response to the rare low tone were averaged over a mean of 36 trials (range 23-45) and those in response to the novel sounds (target) were averaged over a mean of 38 trials (range 28-45).

The waveforms (see figure 6.1) showed a negative deflection in all three conditions at approximately 100 ms (N100). This was followed by a positive deflection in response to the novel sounds which was most clearly visible at frontal lateral sites (see figure 6.1) but which was not seen in response to stimuli in either of the other two conditions (P170). At a mean latency of 297 ms at Pz a large positive deflection was seen in the waveform elicited by the novel sounds (P300). From approximately 400 ms onwards a negative deflection was seen at frontal sites and a positive deflection was seen at posterior sites. These deflections were larger in the waveforms elicited by the novel sounds than those elicited by the frequent and rare

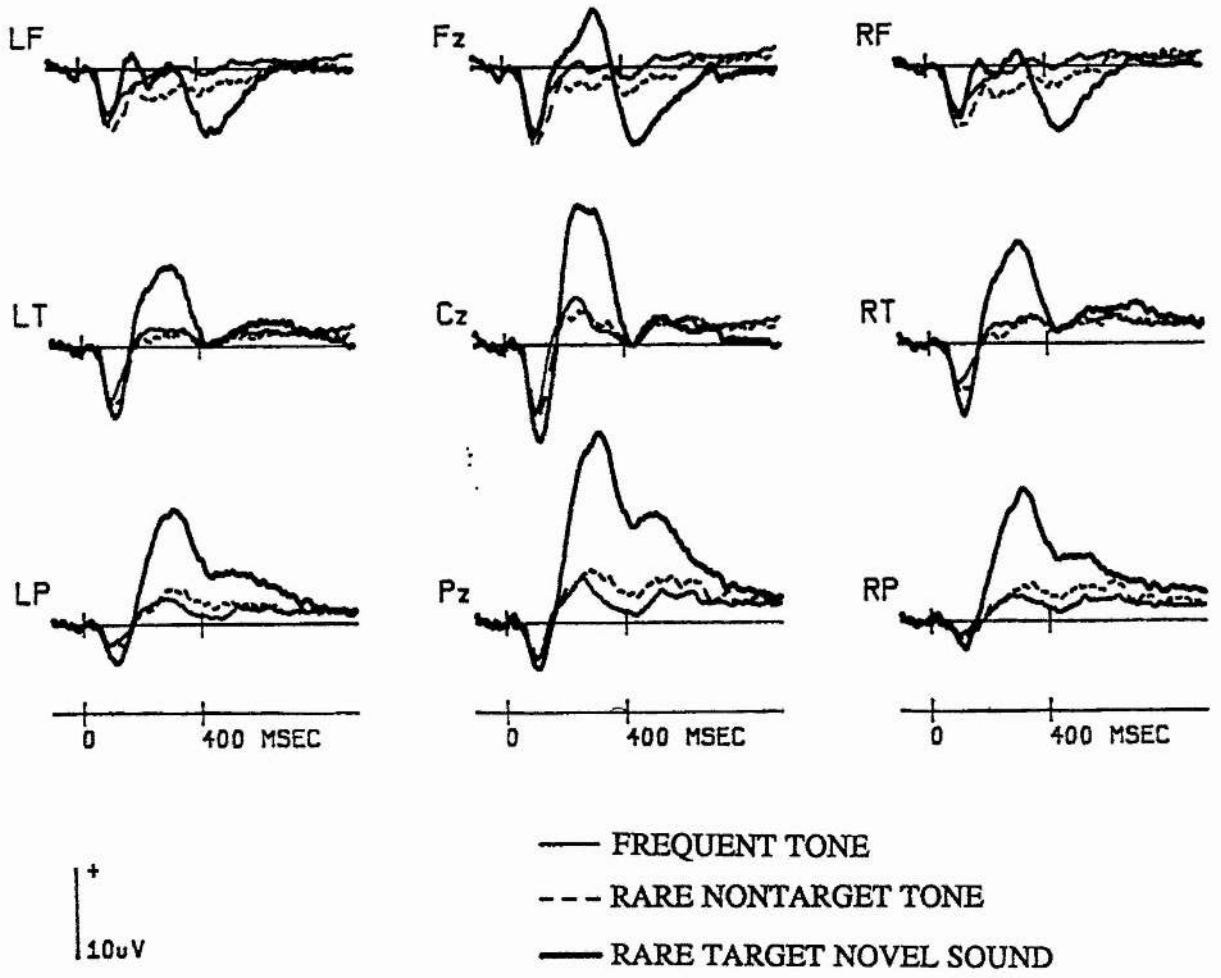


Figure 6.1 Waveforms averaged over 12 subjects for each condition in experiment 3.

tones and were investigated by performing analyses on the mean amplitude of the area of waveform between 400-700 ms. Inspection of the grand average waveforms shows an amplitude difference between the frequent and rare tones at parietal sites from approximately 350-550 ms. This was investigated by performing analyses on the mean amplitude of the area of the waveform between 350-550 ms for the frequent and rare tones.

In order to determine the latency window within which the mean amplitude was to be measured, the peak latency of the N100 was measured at Cz, that of the P170 was measured at Fz and that of the P300 elicited by the novel sounds was measured at Pz. For the novel sound P300 and N100 deflections, measurements could be obtained for all 12 subjects. For the P170, however, measurements could only be made for 7 subjects so the mean latency value of the 7 subjects was used to determine the latency window of the remaining subjects. For the N100, individual latency windows were used for each condition for each subject. The P300 and P170 could only be distinguished in the waveforms elicited by the novel targets. The latency window was therefore determined for the novel target condition for each subject and the same latency window used for the other two conditions. These latency windows will be referred to as the P300 region and P170 region respectively.

Repeated measures 12*3*3*3 (subject*condition*chain*site) ANOVAS were performed on P300, N100, P170 and 400-700 ms region data before and after rescaling. A 12*2*3*3 (subject*condition*chain*site) ANOVA was performed on the 350-550 ms region before and after rescaling.

Latencies and amplitudes of the components elicited in the present experiment were compared with those elicited in Experiment 1. To investigate latency differences of

the P300 and N100 elicited in the two experiments a 2*12*2 (experiment*subject*site) and a 2*12*3 (experiment*subject*condition) ANOVA was performed respectively. A t-test was used to investigate differences in P170 latency between experiments. To investigate amplitude differences between the two experiments for the N100 and P170 and 500-900 ms region 2*12*3*3*3 (experiment*subject*condition*chain*site) ANOVAs were performed on the raw and rescaled data. For the P300 2*12*2*3*3 (experiment*subject*condition*chain*site) ANOVAs were performed on the raw and rescaled data.

RESULTS

P300 before rescaling

A positive deflection, with a mean latency of 289 ms at Cz and 297 ms at Pz, was present in the waveforms elicited by the novel target stimuli but not the waveforms elicited by the other two categories of stimuli. This difference was confirmed by statistical investigation. As reported in Table 6.1, a significant effect of condition was obtained ($F(1.4,15.7)=58.24$, $P<0.001$) which post hoc testing confirmed was due to the P300 elicited by the target novel sounds being significantly larger in amplitude than the same region of waveform elicited by the frequent and rare non-target stimuli which did not differ.

Table 6.1 shows a significant main effect of chain which interacted significantly with condition. The interaction was due to the P300 elicited by the novel sounds being larger in amplitude at midline than at lateral sites, whereas the same region of the waveforms elicited by the frequent and rare tones showed no difference in

Table 6.1. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli and the same region of the waveform elicited by the frequent stimuli, before and after rescaling.

RAW AMPLITUDE

Factors	df	F	Prob
Condition (CC)	1.4,15.7	58.24	0.000*
Chain (CH)	1.9,20.5	20.35	0.000*
Site (ST)	1.0,11.5	29.99	0.000*
CC*CH	2.4,26.4	16.83	0.000*
CC*ST	1.3,14.0	24.35	0.000*
CH*ST	2.1,22.6	2.19	0.135
CC*CH*ST	2.9,31.4	0.86	0.465

RESCALED AMPLITUDE

Factors	df	F	Prob
Condition (CC)	1.6,17.1	0.15	0.805
Chain (CH)	1.5,16.9	9.41	0.003*
Site (ST)	1.0,11.3	21.59	0.001*
CC*CH	2.0,22.5	1.22	0.316
CC*ST	1.2,13.2	1.51	0.247
CH*ST	2.0,21.9	1.68	0.211
CC*CH*ST	3.2,35.1	0.39	0.775

* indicates statistical significance at the 0.05 level or better

amplitude between the three chains of electrodes. (Newman Keuls test comparing amplitude across chain for each condition separately).

A significant main effect of site was obtained which interacted significantly with condition. Post hoc tests showed that the amplitude of the P300 elicited by the novel targets and the same region of waveform elicited by the rare tones increased from frontal to central and parietal sites which did not differ. In contrast, the same region of waveform elicited by the frequent stimuli showed no difference across site.

P300 after rescaling

As can be seen from Table 6.1, a significant main effect of chain was obtained which post hoc testing showed was due to the P300 region being distributed maximally over midline sites (Newman Keuls comparing amplitude across chain collapsed over site and condition).

A significant main effect of site was obtained. Post hoc tests showed that the distribution of the P300 over central and parietal sites did not differ but was greater at both sites than over frontal electrodes (Newman Keuls comparing amplitude across site collapsed over condition and chain). Table 6.1 shows that no significant condition by site or condition by chain interaction was obtained, indicating that there were no significant differences in scalp distribution between conditions.

N100 before rescaling

An N100 was elicited by stimuli in all 3 conditions. This negative deflection had a mean latency over the three conditions of 108 ms at Cz.

As shown in Table 6.2 of the appendix, the results of the ANOVA are very similar to those obtained for the N100 in Experiment 1.

N100 after rescaling

The results of the analysis of the ANOVA on the rescaled amplitude of the N100 are shown in Table 6.2 of the appendix.

As in Experiment 1, a significant main effect of chain was obtained because the N100 was distributed maximally over the midline (Newman Keuls comparison of amplitude across chain collapsed over condition and site).

A significant condition by site interaction was obtained which, as in experiment 1, was due to the novel sounds (targets) producing an N100 with a central maximum compared with the frontal/central maximum produced by the frequent and rare tones.

A significant interaction was found between condition, chain and site. This was because the rare and frequent tones showed a fronto-temporal maximum at midline and left hemisphere sites but a frontal maximum at right hemisphere sites. For the novel sounds the distribution of amplitude did not differ between the three chains of electrodes with a central maximum being found over each.

P170 before rescaling

A P170 was elicited by the novel target sounds which had a mean latency of 183 ms at Fz. The results of the ANOVA on the amplitude of the P170 region are shown in Table 6.3 of the appendix.

A significant difference in P170 amplitude was found between conditions. As in Experiment 1, this effect was produced because the amplitude of the P170 elicited by the novel sounds was significantly larger than that elicited by the frequent and rare tones which did not differ (Newman Keuls comparison of amplitude across condition collapsed over site and chain).

As shown in Table 6.3 of the appendix, significant main effects of chain and site were obtained. Unlike Experiment 1, no interactions were found with condition. For all conditions, amplitude of the P170 was found to be maximal at central and parietal sites.

P170 after rescaling

Table 6.3 of the appendix shows significant main effects of chain and site were obtained in the analysis of the rescaled data. A significant chain by site interaction was obtained because the P170 was distributed maximally over the midline at central and parietal sites but showed no difference in amplitude between electrode chains at frontal sites.

Table 6.5 Mean amplitude, from 12 subjects, of the 400-700 ms region of the waveforms elicited by the frequent tones, target novel sounds and rare nontarget tones for each site, of each electrode chain (collapsed over sequence).

CONDITION	MIDLINE			LEFT			RIGHT		
	F	C	P	F	C	P	F	C	P
FREQUENT TONES	0.6	1.9	2.4	0.4	1.3	1.4	0.8	2.5	2.1
RARE NONTARGET TONES	-1.0	1.9	4.0	-1.2	1.0	2.1	-0.5	2.3	3.4
TARGET NOVEL SOUNDS	-4.8	1.9	9.7	-3.6	1.9	5.2	-3.4	3.3	6.3

Table 6.7. Mean reaction time (ms) to respond to target novel sound, mean number of hits, mean number of false alarms and corresponding standard deviations (SD) in auditory oddball task of experiment 3.

	MEAN	SD
Reaction time	422.4	139.8
Number of hits	45.0	0.0
Number of false alarms	0.8	1.2

400-700 ms region before rescaling

Table 6.4 of appendix shows the results of the ANOVA on the mean amplitude of the 400-700 ms region. A significant interaction was obtained between condition and site. This interaction was due to the 400-700 ms region of the waveforms elicited by the novel sounds being more negative at frontal sites and more positive at parietal sites than the same region elicited by the two categories of tones.

A significant condition by chain by site interaction was produced. The pattern of the means, shown in Table 6.5, suggest that the interaction was produced because the 400-700 ms region had a parietal maximum at all electrode chains in response to the novel sounds, a centro-parietal maximum at lateral sites and parietal maximum at midline sites in response to the rare tones and a centro-parietal maximum at lateral sites and a frontal maximum at midline sites in response to the frequent tones.

400-700 ms region after rescaling

Table 6.4 of appendix shows a significant chain by site interaction remained in the analysis of the rescaled data. This interaction was obtained because the 400-700 ms region was distributed maximally over parietal sites at the midline but showed no significant differences between sites laterally.

350-550 ms region before rescaling

Table 6.6 of appendix shows the results of the ANOVA comparing the amplitude of the waveforms elicited by the frequent and rare tones between 350 and 550 ms. It can be seen that no significant main effect of condition was obtained.

Significant main effects of chain and site were found and will be discussed in relation to the analysis of the rescaled data.

A significant interaction was obtained between condition and site. Post hoc testing showed that the 350-550 ms region of waveform elicited by the frequent tones did not differ in amplitude between sites, whereas, the same region of the waveforms elicited by the rare tones did not differ in amplitude between central and parietal sites but was larger at both than at frontal sites. Inspection of the mean amplitudes of this region suggested that the 350-550 ms region elicited by the rare tones was more negative at frontal sites and more positive at parietal sites than the same region of waveform elicited by the frequent stimuli. These differences were found not to be statistically significant (Newman Keuls tests comparing amplitude across condition for each site).

350-550 ms region after rescaling

The results of the ANOVA on the rescaled amplitude of the 350-550 ms region are shown in Table 6.6 of appendix. A significant main effect of chain was found which was obtained because the 350-550 ms region was more positive over right than left hemisphere sites but did not differ significantly between midline and lateral sites (Newman Keuls comparison of rescaled amplitude across chain collapsed over condition and site).

A significant main effect of site was obtained. The rescaled amplitude of the 350-550 ms region was distributed more over central and parietal sites than over frontal sites. No significant difference in distribution was found between central and

parietal sites (Newman Keuls comparison of rescaled amplitude across site collapsed over condition and chain).

Behavioural data

Behavioural results are summarised in Table 6.7.

Between experiment comparisons

P300

The ANOVA comparing the latency of the P300 elicited by novel sounds at Cz and Pz, in run 1 of Experiment 1 and in the present experiment, showed a significant effect of site ($F(1,22)=5.229$, $P<0.05$) due to the latency being longer at Pz than Cz. No significant main effect of experiment or experiment by site interaction was obtained. The ANOVA comparing the latency of the P300, elicited by tone targets in Experiment 1 and novel targets in the present experiment, showed a significant main effect of experiment, due to the longer latency of the P300 elicited by the target tones, and a significant main effect of site, due to the longer latency of the P300 elicited at Pz compared with that at Cz. No significant experiment by site interaction was obtained.

An ANOVA was performed comparing the amplitude of the P300 elicited by the targets and rare nontargets in Experiment 1 and the present experiment. A significant main effect of experiment was obtained ($F(1,22)=6.539$, $P<0.05$) which was due to the amplitude of the P300 elicited in Experiment 1 being significantly larger than that elicited in the present experiment.

A significant interaction was found between experiment, condition and chain ($F(2.0,43.6)=4.281$, $P<0.05$) before and ($F(1.9,42.2)=6.139$, $P<0.005$) after rescaling. This interaction was produced because the P300 elicited by the rare tones showed no significant difference in amplitude across the electrode chains for both experiments. In contrast the P300 elicited by the novel sounds had a midline maximum in both experiments but the difference in P300 amplitude between midline and lateral sites was not as large in the present experiment as in Experiment 1. In addition, the P300 elicited in the present experiment was distributed more over right than left hemisphere sites, whereas that elicited in experiment 1 showed no differences in amplitude between lateral sites.

A significant experiment by condition by site interaction was obtained ($F(1.2,26.4)=23.758$, $P<0.001$) before and ($F(1.2,26.2)=10.765$, $P<0.005$) after rescaling. This was produced because the P300 elicited by the novel sounds had a more parietal distribution in the present experiment than in Experiment 1. The same region of the waveform elicited by the rare tones showed no difference in amplitude at frontal and parietal sites between the two experiments but was larger at central sites in the present experiment than in experiment 1. This interaction is illustrated in Figure 6.2.

A 2*12*3*3 (experiment*subject*chain*site) ANOVA comparing the amplitude of the P300 elicited by the novel sounds in Experiment 1 and the present experiment showed a significant experiment by site interaction. This was obtained because the amplitude of the P300 elicited in the present experiment was significantly smaller at frontal sites than that elicited in Experiment 1 but did not differ significantly between experiments at other sites.

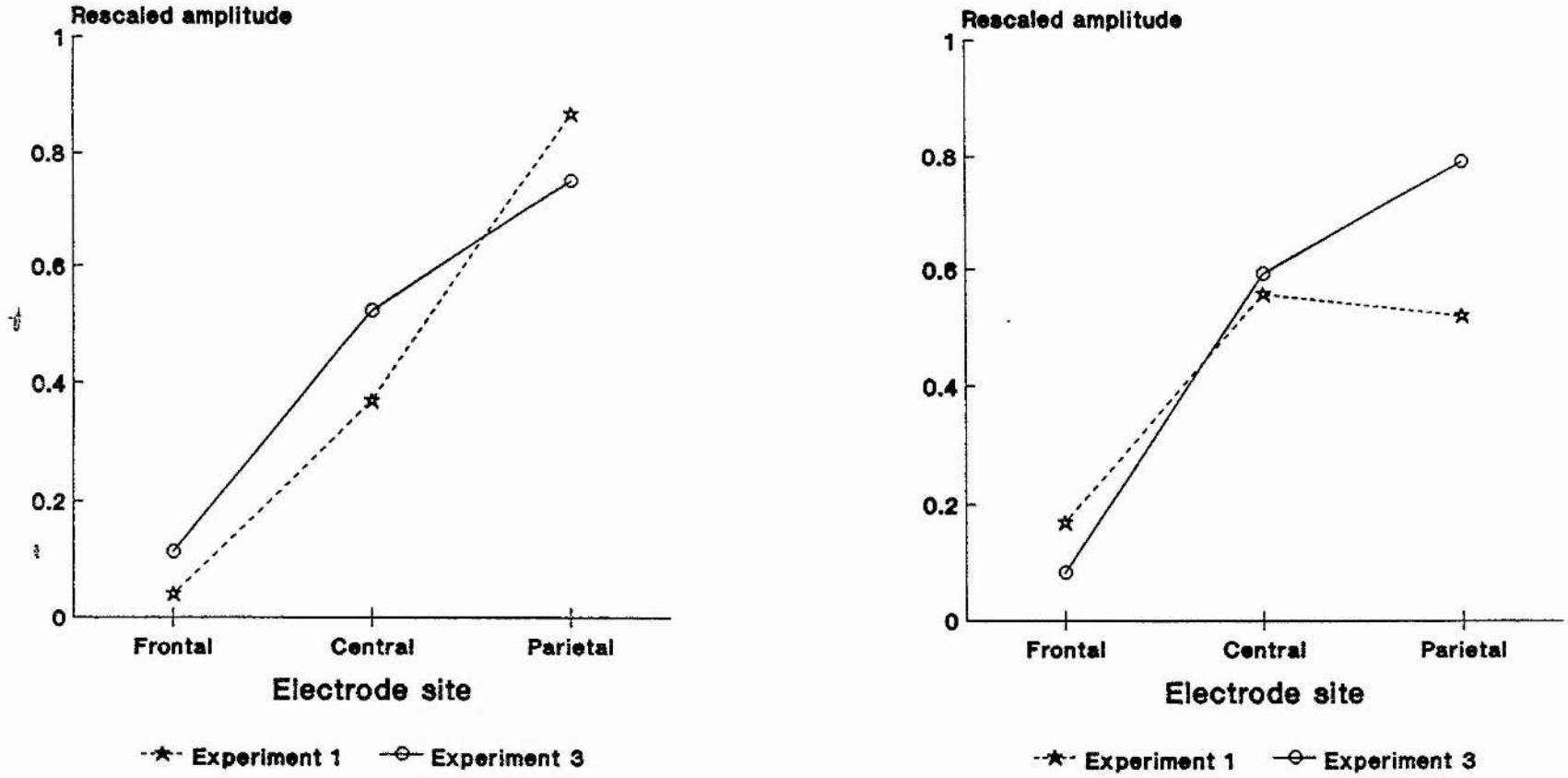


Figure 6.2 Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by the target tones and novel sounds in experiment 1 and experiment 3.

500-900 ms

The mean amplitude of the 500-900 ms region of the waveform elicited in the present experiment and experiment 1 was compared, as changes in the scalp distribution of the P300 between experiments may have been due to changes in overlapping slow wave activity. The results of the ANOVA comparing the 500-900 ms region between the two experiments shows no significant effects of experiment in the analysis before or after the data was rescaled.

Summary of Results

P300 evoked by the novel sound targets was significantly larger in amplitude than the same region of waveform evoked by the frequent and rare nontarget stimuli. The P300 region of waveform was found to be distributed maximally over parietal and central sites for all three conditions. In response to the novel sound targets, the P300 was significantly larger at midline than at lateral sites which did not differ. For the rare nontarget tones and frequent tones the same region of waveform showed no differences between chains. N100 showed no significant amplitude differences between conditions. N100 was found to be significantly larger at midline than at lateral sites. The N100 in response to the novel targets had a central maximum, whereas that in response to the frequent and rare tones had a central/frontal maximum. P170 was found to be significantly larger in response to the novel sound targets than the frequent and rare tones. P170 was significantly larger at midline than at lateral sites which did not differ and was distributed maximally over parietal and central sites. The 400-700 ms region was found to be more negative at frontal sites and more positive at parietal sites in the waveforms elicited by the novel

sounds than those elicited by the two categories of tones. The amplitude of the 350-550 ms region of waveforms elicited by frequent and rare tones did not differ significantly between condition. Amplitude of the 350-550 ms region was significantly larger over right than left hemisphere sites but amplitude at the midline did not differ significantly from that over either hemisphere.

DISCUSSION

P300

The results of the present experiment do not clearly distinguish between the proposals discussed in the Introduction. The first proposal suggested that the centro-parietal distribution of the P3a found in Experiment 1, may result from the overlap of anteriorly and posteriorly distributed activity. The anterior activity was thought to result from the detection of a mismatch, by the passive preattentional comparison process, between the features of the presented stimulus and those of the frequent stimulus held in sensory memory. The posterior activity was thought to be activated by stimuli requiring a response. It was suggested that when a novel nontarget sound was presented both types of activity were present. The anterior because the novel sound was sufficiently different from the frequent stimulus and the posterior because the subjects treated the task as a go/no-go task having to inhibit a button press response to the novel sounds. It was therefore suggested that, if the same stimulus sequence was used, the scalp distribution of the P3 elicited by the novel sounds would be the same when their presentation required a button press as when no physical response was necessary.

The results showed the generation of a centro-parietally distributed P3 in response to the target novel sounds which supports the above suggestion. The distribution of the P3 elicited by the novel sounds when targets was, however, more parietal than that elicited by the rare nontarget novel sounds of Experiment 1. It is possible that the extent to which a centro-parietal versus a parietal maximum is obtained, depends on the strength of activation of the generators producing anterior and posterior activity. It could be suggested that in the present experiment there is more activity of the generator(s) producing posteriorly distributed activity in response to the target novel sounds than it was when they were rare nontargets in Experiment 1. Alternatively, the more parietally maximal P300 elicited by the target novel sounds may have been produced because of the overlap of a posterior positive slow wave onsetting within the P300 latency range. This is unlikely, however, because the amplitude of the 500-900 ms region did not differ significantly between the two experiments.

The amplitude of the P3a, elicited by rare nontarget novel sounds in Experiment 1, was significantly larger than that elicited by the novel sounds when targets in the present experiment. The decrease in amplitude was found at frontal sites with no decrease at central and posterior sites. This suggests that when the novel sounds are assigned signal value, there may be a relative decrease in the activation of the more anterior generator.

The alternative hypothesis discussed in the Introduction was that the centro-parietal P300, elicited by the rare nontarget novel sounds of Experiment 1, was obtained because the sounds were no-go stimuli and that all no-go stimuli will produce a P300 with this distribution. For the go stimuli a P300 with a parietal maximum is produced. It is therefore possible that the P300 produced by the novel sounds was more parietally distributed in the present experiment than in Experiment 1 because

the stimuli were now targets (go stimuli). The P300 elicited by the target novels was, however, differently distributed across the three electrode chains to that elicited by the target tones of Experiment 1. The P300 elicited by the target novels had a midline maximum like that obtained when the novel sounds were nontargets, whereas that elicited by the target tones did not differ in amplitude across electrode chains. This finding suggests, therefore, that there may be a contribution to the waveform elicited by the novel targets that was not present for the target tones. The presence of an additional contribution to the waveform elicited by the novel targets is supported by the larger amplitude P300 elicited by the novel targets than by the tone targets because the target P3b is thought to be independent of stimulus deviance (e.g. Courchesne et al., 1978). It is therefore suggested that the change in scalp distribution, from Experiment 1 to the present experiment, of the P300 elicited by the novel sounds does not simply reflect the change in activation from no-go to go generator(s).

No difference was found between the frequent and rare tones in the amplitude of the region of waveform corresponding to that +-12 ms around the P300 elicited by the novel targets which suggests that subjects may be using a different strategy from that used in previous tasks. Subjects may be using a strategy in which they respond whenever a tone is not presented and so treat the high and low tones as one category of no-go stimuli with a probability of 0.85. It is known that the amplitude of the P300 is dependent on the probability of the stimuli, with low probability stimuli eliciting larger amplitude P300s, as the probability of the tones in the present experiment was high they would not be expected to elicit a P300.

Analysis of the 350-550 ms region of waveform, that is, the region in which the amplitude of the waveforms elicited by the frequent and rare tones appeared to

differ, gave results very similar to the analysis of the P300 region. Therefore, even when the region of waveform was investigated in which the frequent and rare tones appeared to differ, there was no significant difference between the two categories of tones.

As will be discussed in more detail in the next experiment, it is possible that detection of a mismatch between the features of the frequently occurring stimulus and the present stimulus is not the only route available during a one channel oddball task for the detection of target stimuli and the elicitation of the P3b. It is possible that, in addition, the targets can be detected by a more active process such as the detection of a match between the features of the presented stimulus and those of a template of the target stimulus (e.g. Naatanen, 1990). It may be that only the novel sounds in Experiment 1 were deviant enough from the frequent stimuli to gain access to central processing via the passive mismatch detection route, the target tones may gain access via a different route. Since both stimuli had gained access to central processing a go/no-go response would be made as appropriate. In the present experiment it could be argued that the rare tones do not gain access to central processing because they do not sufficiently mismatch the sensory trace of the frequent stimulus and do not match the actively maintained trace of the target stimulus. In contrast, the novel sound targets will gain access to central processing via both or either of these routes. Adoption of a template matching process for the detection of the target novel sounds may affect the threshold of the passive mismatch detection process and therefore may affect the strength of activation of the generator(s) producing anteriorly distributed activity.

N100

As seen in the results section, no significant differences were found in the N100 between Experiment 1 and the present experiment. The N100 was found to have a frontal/central maximum in response to the frequent and rare tones and a central maximum in response to the novel sounds which was as found in Experiment 1. These findings suggest that the process reflected by the N100 is responsive to the physical characteristics of the stimuli and possibly their relation to other stimuli in the sequence. In contrast, it appears to be unaffected by the psychological processes active in the task including such factors as the role of the stimulus e.g. whether it requires a response.

P170

The P170 was found to have a centro-parietal maximum in all conditions which was due to its superimposition on the rising slope of the P3 wave. This made it difficult to investigate differences in P170 between conditions. Inspection of the grand average waveforms shows a larger P170 in response to the novel sounds than the other stimuli. This is particularly noticeable at frontal lateral sites, probably because the influence of the P3 is less here. The novel sounds, when rare nontargets in Experiment 1, elicited a larger P170 than the other stimuli. This suggests that the role of the stimulus in the task ie. whether it requires a response or not does not affect the occurrence of the P170. The results of the present experiment are consistent with ideas of the functional significance of the P170 discussed in the previous two experiments.

400-700 ms region

Following the P300 a negative deflection was found at frontal sites and a positive deflection at parietal sites in the waveform elicited by the novel targets but not those

of the frequent and rare tones. The deflections may be components of the 'O' wave discussed by Rohrbaugh and Gaillard (1983). The 'O' wave refers to a complex of waves elicited by the initial stimulus in a CNV paradigm or stimuli presented singly in, for example, an oddball paradigm. The complex consists of the P300, a slow negative wave peaking at frontal sites with a latency of 500-700 ms (SNW1), a positive slow wave with the same or slightly earlier latency and a parietal maximum (SPW) and a late broadly distributed negative slow wave (SNW2). It is possible that the deflections seen in the waveforms elicited by the novel targets may be the SNW1 and SPW. In Experiments 1 and 2 both categories of rare stimuli elicited a slow wave which was negative at frontal sites and positive at parietal sites. In these experiments it has been argued that subjects treat the task as a go/no-go task pressing a button in response to one of the rare stimuli and withholding a response to the other rare stimulus so that both categories of rare stimuli are task relevant. In the present experiment it is suggested that only the novel sounds are task relevant and that the other stimuli in the task do not gain access to central executive processes. The novel sound targets will, therefore, be the only stimuli which require further processing as reflected by the slow waves.

In summary, the results presented here do not provide clear support for either of the hypothesised explanations for the generation of a centro-parietal P300 in response to novel sounds in Experiment 1. The amplitude and distribution of the P300 elicited by target novel sounds suggests the contribution of processes additional to those involved in generating the P3b to target tones. The centro-parietal distribution of the P300 to novel sounds in experiment 1 was proposed to result from the overlap of posterior and more anterior activity. The P300 elicited by novel targets was more parietally distributed than that elicited by rare nontarget novel sounds and it was suggested that this may be due to the relative strength of activation of the two

generators differing between the two experiments. The results concerning the N100 and P170 are consistent with the suggestions for their functional significance discussed in the previous two experiments. The frontal negative and posterior positive slow waves were found only to be elicited by the target novel sounds in the present experiment. This is consistent with the proposal that the slow waves reflect further processing of task relevant stimuli.

CHAPTER 7

EXPERIMENT 4: THE EFFECT OF OMISSION OF THE FREQUENT STIMULI ON THE OCCURRENCE OF THE P3A

INTRODUCTION

As discussed in Chapter 1 (General Introduction), Naatanen (1990) has proposed that, in a one channel oddball task, conscious discrimination of a stimulus is initiated by the detection of a mismatch between the features of the presented stimulus and those of the frequently occurring stimulus held in sensory memory. The P3a is thought to reflect processes involved in the orienting of attention, that is, enabling access to processing which leads to conscious discrimination of the stimulus. In contrast, the P3b is thought to reflect further processing of stimuli which, once consciously discriminated, are found to be significant in the task. Naatanen (1990) suggests that, in a one channel oddball paradigm, detection of a mismatch with the trace held in sensory memory is necessary for the elicitation of both the P3a and the P3b.

The necessity of mismatch detection for the generation of the P3a and P3b was investigated in the two experiments reported here. In Experiment 4A, subjects were presented with one of the stimulus sequences from Experiment 1 but with the frequent stimuli omitted. The frequents were replaced with a gap of equivalent duration so that the temporal interval between target and deviant nontarget stimuli remained the same as in the first experiment. It was predicted that, as the stimuli did not occur frequently enough for a trace to be present in sensory memory, when the next stimulus was presented there would be no representation against which the

presented stimuli could mismatch. As it is proposed that mismatch detection is necessary for the elicitation of the P3a and the P3b (Naatanen 1990), neither of these components would be expected to be elicited in the present experiment. Experiment 4B allowed a within subject comparison of the ERPs elicited by stimuli in the task used in Experiment 1 and that used in Experiment 4A. It was proposed that a P3a would be elicited in response to the novel sounds and a P3b elicited in response to the target tones in the task of Experiment 1 ('frequents present' task). In the task of Experiment 4A ('omitted frequents' task) neither of these components would be produced.

EXPERIMENT 4A

METHOD

Subjects

Twelve healthy subjects (mean age 19, range 18-20 yrs, 7 female) were tested. All were paid volunteers.

Design

One of the stimulus sequences of Experiment 1 was used. The frequent tones, however, were omitted so that only the target tone and the rare nontarget novel sounds were presented. The (irregular) temporal separations between the occurrences of these stimuli were identical to those in Experiment 1; thus the temporal probability of the stimuli was unchanged from the first experiment.

Procedure

Subjects were presented with a sequence of stimuli from Experiment 1 but with the frequents omitted. The sequence therefore consisted of occasional low tones and novel sounds each with a sequential probability (probability of a particular stimulus within a certain number of stimuli) of 0.5 but with the same temporal probability (probability of a particular stimulus within a certain period of time) as in Experiment 1 i.e. 0.15. The subject was instructed to press a button with the preferred hand in response to the tone and to do nothing in response to the other sounds. A sequence of practice trials were presented to ensure that the target tone could be confidently detected. The experimental trials were presented in 3 blocks which occupied the same temporal interval as in Experiment 1. A 30 s break was given between each block.

DATA ANALYSIS

As in Experiment 1 separate averages were obtained for each experimental condition. The waveform in response to the targets was averaged over a mean of 30 trials (range 16-43) and that in response to the nontarget novel sounds was averaged over a mean of 30 trials (range 15-42). The mean amplitudes of the N100, P170, N200 and P300, as defined in Experiment 1, were obtained for the area of waveform +-12 ms round the peak. For the N100, the latency window was determined for each subject by measuring the N100 peak latency for both stimulus conditions at Cz. The latency window for the P170 was determined by measuring the peak latency for the

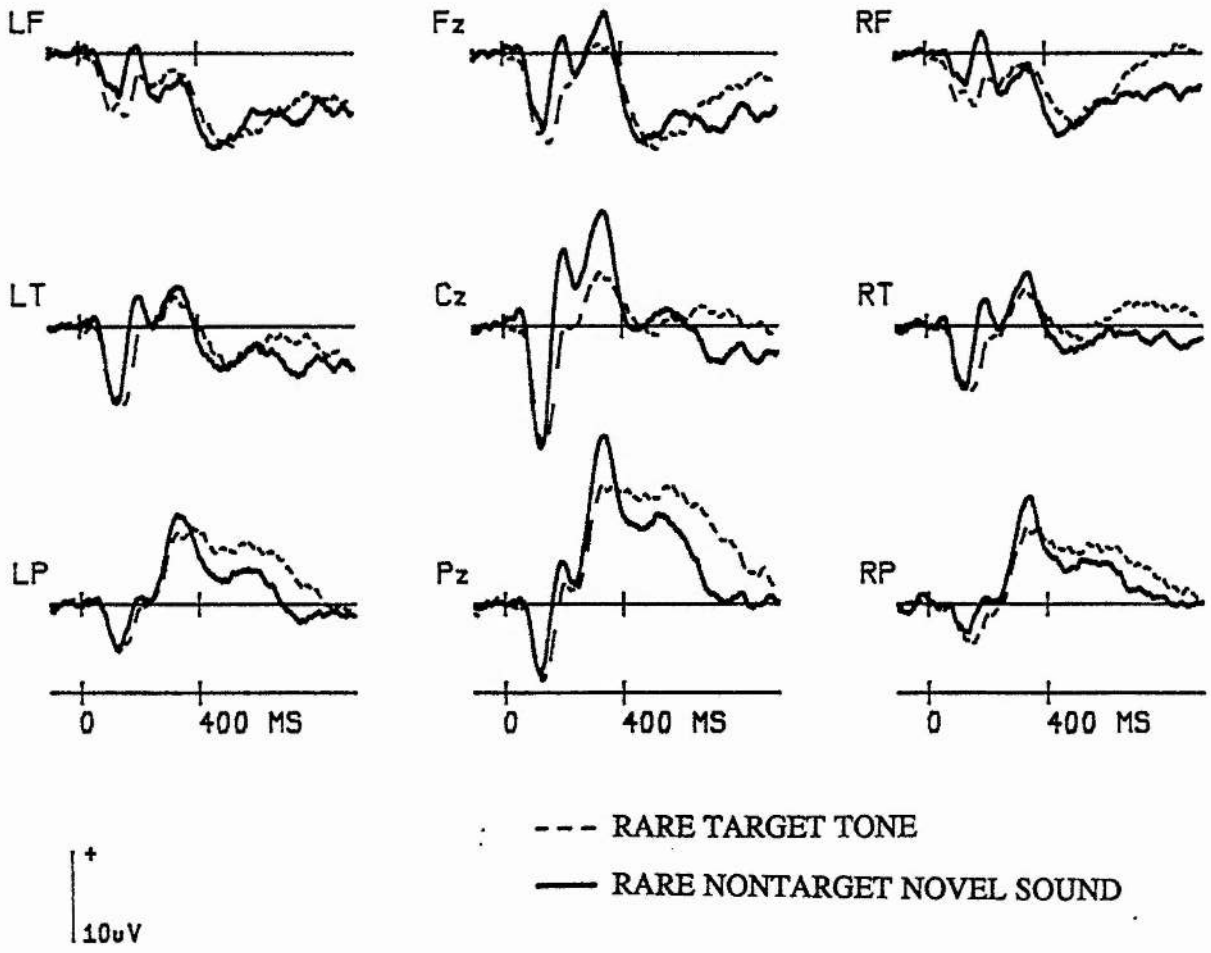


Figure 7.1 Waveforms averaged over 12 subjects for the two conditions of experiment 4a.

response to the rare novel sounds at Fz for each subject. For the P300 the latency window was determined for each subject in the same way as in Experiment 1.

A 12*2*3*3 (subject*condition*chain*site) ANOVA was carried out for each peak comparing the response elicited by the target and nontarget novel sounds before and after the data was rescaled.

A 2*12*2*3*3 (experiment*subject*condition*chain*site) ANOVA was carried out on the raw and rescaled data of each peak for the two experiments. This allowed the comparison of amplitude changes and the scalp distributions of the responses elicited by the targets and nontarget novel sounds in the two experiments.

RESULTS

P300 before rescaling

As shown in the waveform (Figure 7.1) a positive peak with a mean latency of 366.7 ms (SD=47) at Pz and 353 ms (SD=52.4) at Cz was obtained in response to the targets. These latencies did not differ significantly ($t=-0.58$, $P>0.05$). The rare nontarget novel sounds elicited a positive deflection with a mean latency of 351 ms (SD=46.8) at Pz and 354 ms (SD=46.6) at Cz. These latencies did not differ significantly ($t=1.6$, $P>0.05$). No significant difference in the latency of the P300 deflection was found between targets and novel sounds at either Cz ($t=-0.06$, $P>0.05$) or Pz ($t=0.76$, $P>0.05$).

Table 7.1 shows the results of the ANOVA on the P300 amplitude data. It can be seen that a significant interaction was obtained between condition and chain. Post hoc testing showed that this was produced because the P300 elicited by the novel sounds was significantly larger than that elicited by the target tones at midline but not at lateral sites. This amplitude difference was found because the P3 elicited by the novel sounds showed a midline maximum amplitude, in comparison the P300 elicited by the targets did not differ in amplitude across electrode chain.

A significant main effect of site was obtained. The amplitude of the P300, elicited by stimuli in both conditions, was found to be significantly larger at parietal than central sites and larger at central than at frontal sites.

P300 after rescaling

Table 7.1 shows that a significant main effect of chain was obtained in the ANOVA on the rescaled data. Newman Keuls tests comparing rescaled amplitude across chain, collapsed over condition and site, showed the P300 to be distributed significantly more over midline than lateral sites which did not differ. No significant interactions were obtained with chain.

A significant main effect of site was obtained which confirmed the parietal maximal distribution of the P300 suggested by the results of the ANOVA on the raw amplitude data.

As shown in Table 7.1, no significant interaction was obtained between condition and site after rescaling. This indicates that there was no difference in the scalp distribution of the P300 elicited by target and rare deviant nontarget stimuli. The

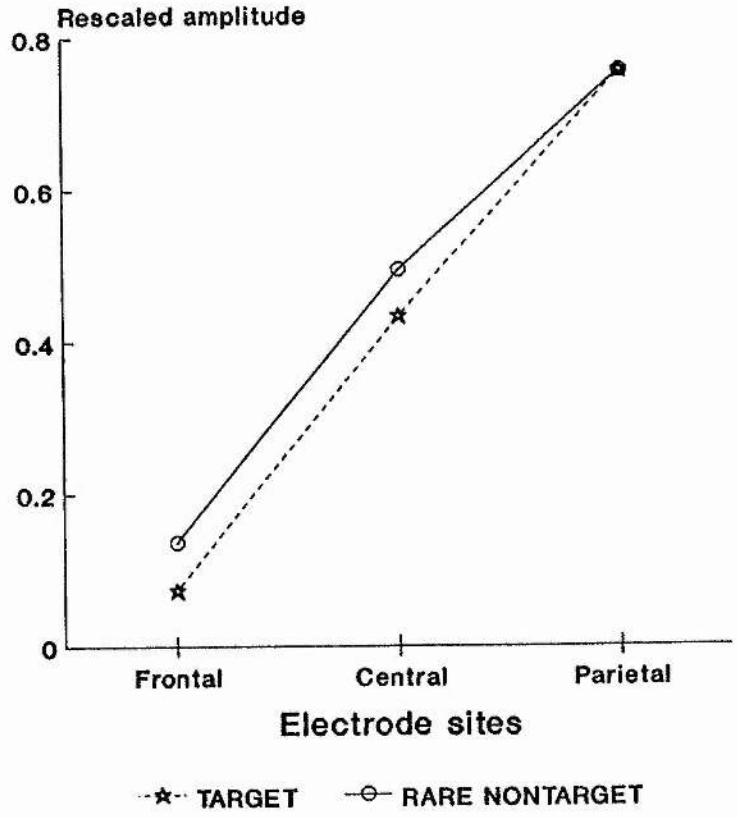
Table 7.1. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Condition (CC)	1,11	1.15	0.307
Chain (CH)	1.8,19.5	32.22	0.000*
Site (ST)	1.4,15.5	59.54	0.000*
CC*CH	1.7,19.1	6.29	0.010*
CC*ST	1.1,11.8	0.97	0.349
CH*ST	3.3,36.7	2.09	0.112
CC*CH*ST	2.3,25.8	1.69	0.201

RESCALED AMPLITUDE			
Factors	df	F	Prob
Condition (CC)	1,11	0.25	0.627
Chain (CH)	1.7,19.2	31.52	0.000*
Site (ST)	1.4,15.4	57.61	0.000*
CC*CH	1.8,19.9	2.03	0.162
CC*ST	1.1,11.9	0.38	0.561
CH*ST	3.3,36.2	2.18	0.102
CC*CH*ST	2.3,25.2	2.03	0.147

* indicates statistical significance at the 0.05 level or better

Figure 7.2 Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by the two categories of stimuli in experiment 4a (distribution at midline sites plotted only).



scalp distribution of the P300, elicited by stimuli in the two conditions, is graphed for the midline sites in Figure 7.2.

N100 before rescaling

As shown in Table 7.2 of Appendix, the results of the ANOVA on the amplitude of the N100 elicited by the targets and rare nontarget novel sounds were similar to those obtained for Experiment 1. No significant difference in N100 amplitude was found between conditions. Significant main effects of chain and site were obtained which are discussed in relation to the analysis of the rescaled data.

N100 after rescaling

The results of the analysis of the rescaled data are given in Table 7.2 of Appendix. As in Experiment 1, a significant main effect of chain was found because the N100 was distributed maximally over midline sites.

A significant main effect of site was obtained. Newman Keuls tests showed that the N100 elicited in both conditions was significantly larger at central sites than at parietal or frontal sites which did not differ significantly. Unlike Experiment 1, no significant interaction was found with condition.

P170 before rescaling

The results of the ANOVA are given in Table 7.3 of Appendix. As in Experiment 1, the P170 elicited by the rare nontarget novel sounds was significantly more positive

than that elicited by the targets. The significant interactions obtained will be discussed in relation to the analysis of the rescaled data.

P170 after rescaling

The results of the ANOVA on the rescaled P170 data are shown in Table 7.3 of Appendix. Unlike Experiment 1, a significant condition by chain interaction was found. Newman Keuls tests showed that this was produced because the P170 elicited by the targets was distributed evenly over the three chains of electrodes, whereas, that elicited by the novel sounds was significantly larger at the midline than over the right and left hemispheres which did not differ.

A significant condition by site interaction was obtained. Newman Keuls tests showed no significant difference between conditions in the distribution of the P170 across site. The distribution of the means, however, suggested that the target P170 had a more parietal distribution than the P170 elicited by the novel sounds (see Table 7.4). Newman Keuls tests comparing the difference in rescaled P170 amplitude between conditions for each site showed no difference in rescaled amplitude between conditions at frontal and central sites but showed the rescaled amplitude of the P170 elicited by targets to be larger than that elicited by novel sounds over parietal sites.

A significant interaction was found between chain and site. Newman Keuls tests showed that this was because at frontal and central sites no significant differences were found between chains whereas at parietal sites P170 was significantly larger at the midline than over both left and right hemispheres which did not differ.

Table 7.4 Mean rescaled amplitude, from 12 subjects, of the P170 deflection elicited by target tones and novel sounds for each electrode site (collapsed over sequence and chain).

CONDITION	FRONTAL	CENTRAL	PARIETAL
TARGET TONE	0.2	0.4	0.7
NOVEL SOUNDS	0.2	0.6	0.2

Table 7.7. Mean reaction time (ms) to respond to target tone, mean number of hits, mean number of false alarms and corresponding standard deviations (SD) in auditory oddball task of experiment 4A.

	MEAN	SD
Reaction time	541.0	104.3
Number of hits	44.0	2.3
Number of false alarms	0.6	1.4

N200 before rescaling

The results of the ANOVA are shown in Table 7.5 of Appendix. It can be seen that there is no significant difference in the amplitude of the N200 elicited in the two conditions. No significant main effect of chain was found and no significant interactions were found with chain.

A significant interaction was found between condition and site. Newman Keuls tests showed that this was produced because the N200 elicited by the targets was significantly more positive at parietal sites than at frontal sites but did not differ significantly between central and parietal sites or central and frontal sites. In contrast, the rare nontarget novel sounds elicited an N200 which did not differ between central and parietal sites but was significantly more positive at both sites than at frontal sites.

N200 after rescaling

As shown in Table 7.5 of Appendix, the only significant main effect was of site, which was due to the N200 being significantly more positive at central and parietal sites than at frontal sites.

A significant condition by chain by site interaction was obtained. Newman Keuls testing showed that at the midline the difference in the N200 between targets and rare nontarget novel sounds was significantly greater at central than at both frontal and parietal sites but that at lateral sites there was no significant difference in the N200 between conditions. This is shown in Figure 7.3.

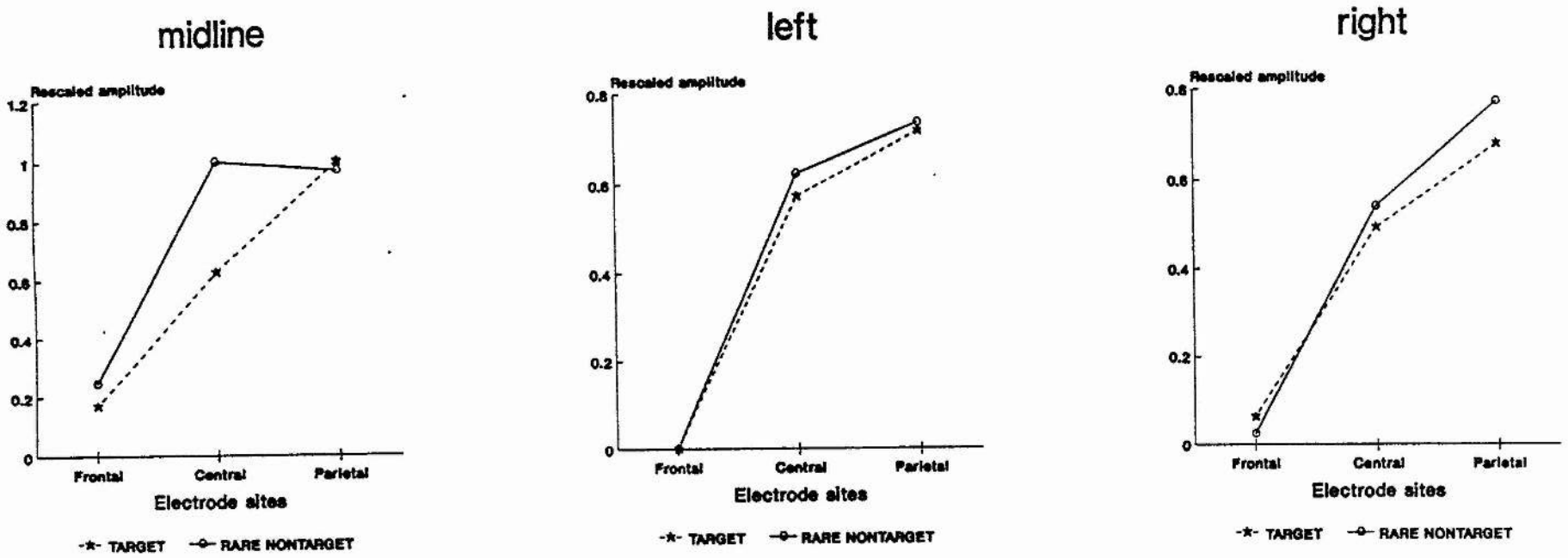


Figure 7.3 Graph illustrating the distribution of rescaled amplitude of the N200 deflection across midline, left and right hemisphere sites for the two categories of stimuli in experiment 4a.

500-900 ms region before rescaling

The results of the ANOVA are given in Table 7.6 of Appendix. As in Experiment 1, no significant main effect of condition was obtained. A significant interaction was obtained between condition, chain and site. The 500-900 ms region of waveforms elicited by the targets was larger than the same region elicited by the novel sounds. Newman Keuls post hoc tests showed that the three way interaction was produced because the difference in the amplitude of the 500-900 ms region between the two conditions was larger at midline than at lateral sites at parietal sites but did not differ between electrode chains at central and frontal sites.

500-900 ms region after rescaling

As shown in Table 7.6 of Appendix, a significant main effect of site was obtained which interacted significantly with chain. The interaction was produced because the 500-900 ms region was found to be of maximum positivity at parietal sites over the midline and left hemisphere but to have a temporal/parietal maximum positivity over the right hemisphere.

Behavioural Measures

Reaction time, number of hits and number of false alarms for responses to the target stimuli are shown in Table 7.7. No significant difference in any of these measures between the two experiments was shown by t-tests.

Between experiment comparisons

P300

ANOVA on the rescaled data comparing the target and deviant P300 elicited in the two experiments revealed a significant interaction between experiment, condition and chain ($F(1.8,40.4)=12.881$, $P<0.001$). This was because the target and deviant nontarget P300s were distributed in the same way across electrode chains in the present experiment, whereas in Experiment 1, the P3a elicited by the novel sounds showed a midline maximum but compared with the P3a, the P3b elicited by the targets did not differ significantly across chains. This is shown in Figures 7.4a and 7.4b. A significant experiment by condition by site interaction was also obtained ($F(1.1,24.3)=7.726$, $P<0.01$). The interaction was produced because the P300 elicited by the targets showed no difference in distribution across site between the two experiments, whereas the P300 elicited by the rare novel sounds showed a centro-parietal maximum in Experiment 1 but a parietal maximum in the present experiment. This is shown in Figures 7.5a and 7.5b.

The change in scalp distribution of the P300 elicited by the novel sounds in the two experiments may be due to the absence of either an overlapping posterior negativity or an anterior positivity in the second experiment. The ANOVA on the P300 amplitude measurements before rescaling showed a significant experiment by condition by site interaction ($F(1.1,24.9)=7.719$, $P<0.001$). This interaction was obtained because the target P300 showed no change in amplitude at any electrode site, whereas the P300 elicited by the rare novel sounds decreased in amplitude at frontal and central sites but showed no amplitude difference at parietal sites between the two experiments (see Figures 7.6a and 7.6b). This suggests that the difference in

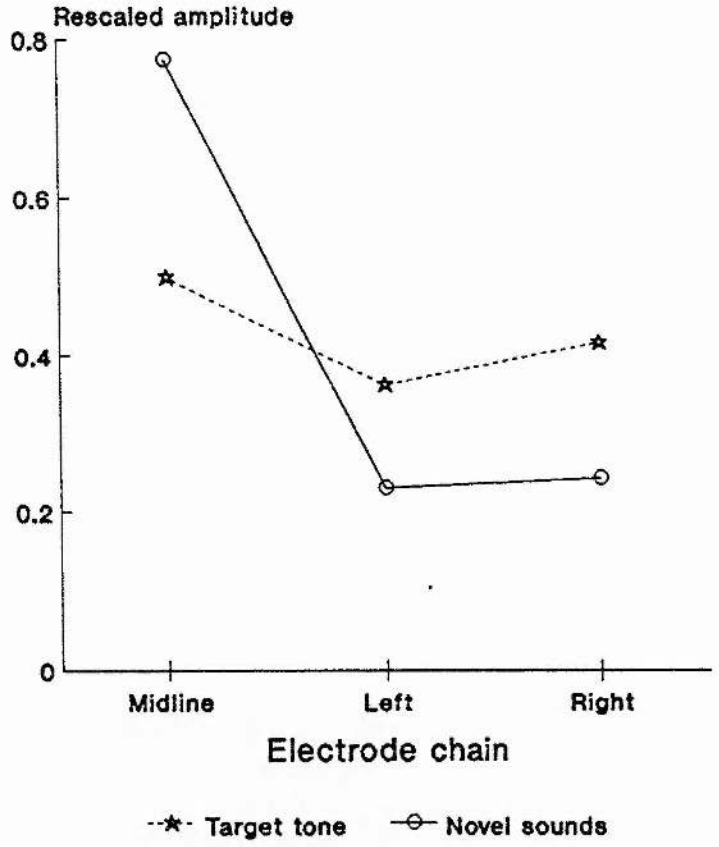


Figure 7.4a Graph illustrating the distribution, across electrode chain, of rescaled amplitude of the P300 deflection elicited by the two categories of stimuli in experiment 1.

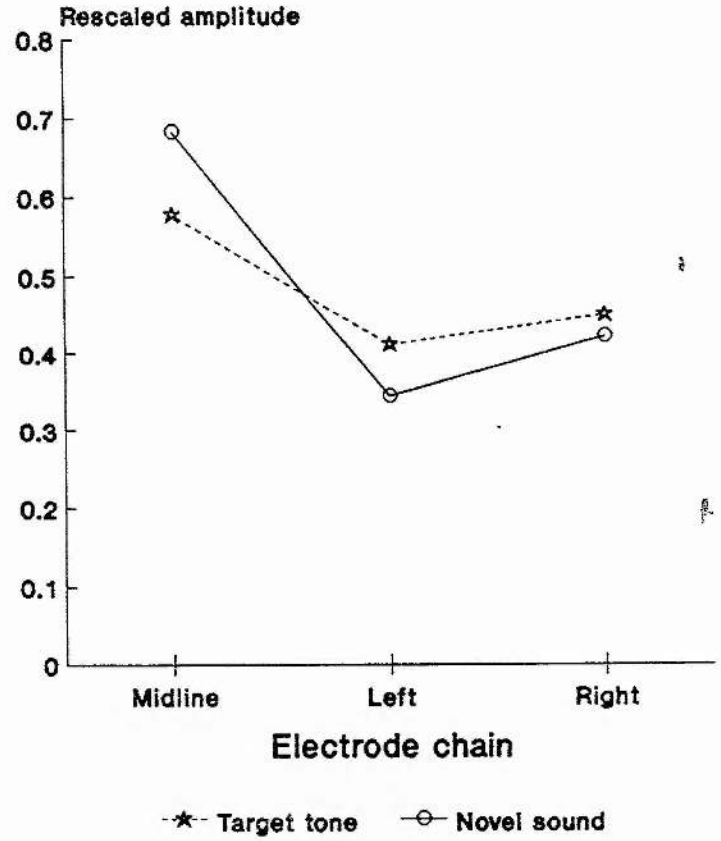


Figure 7.4b Graph illustrating the distribution, across electrode chain, of rescaled amplitude of the P300 deflection elicited by the two categories of stimuli in experiment 4a.

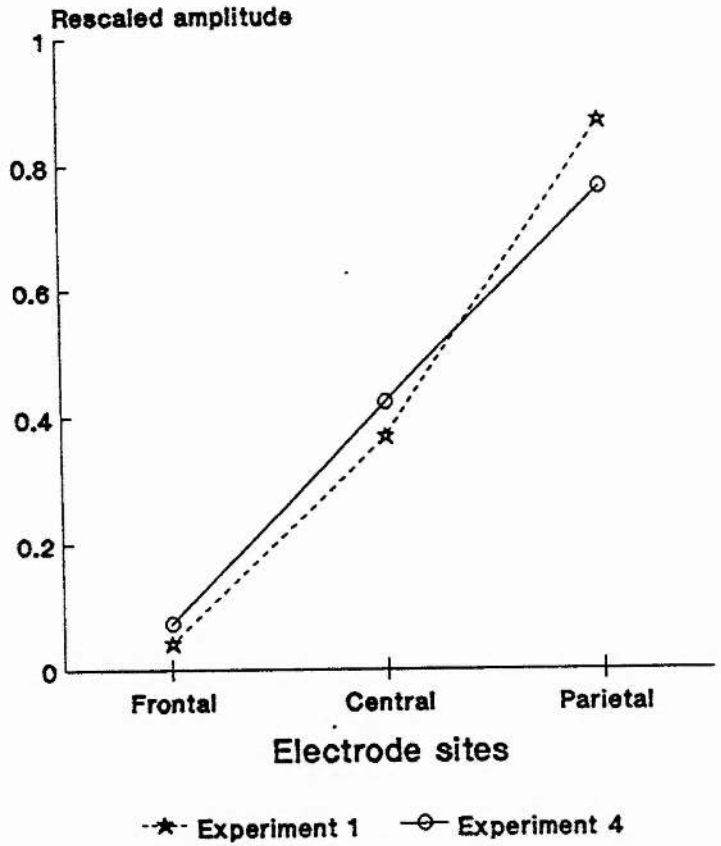


Figure 7.5a Graph illustrating the distribution across site of rescaled amplitude of the P300 deflection elicited by targets in experiment 1 and experiment 4a.

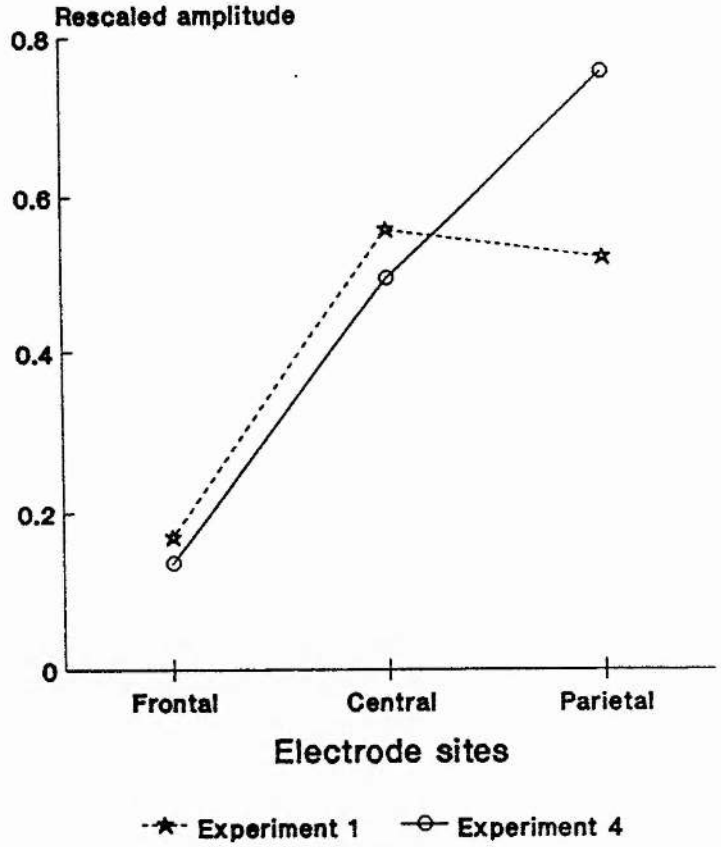


Figure 7.5b Graph illustrating the distribution across site of rescaled amplitude of the P300 deflection elicited by rare nontargets in experiment 1 and experiment 4a.

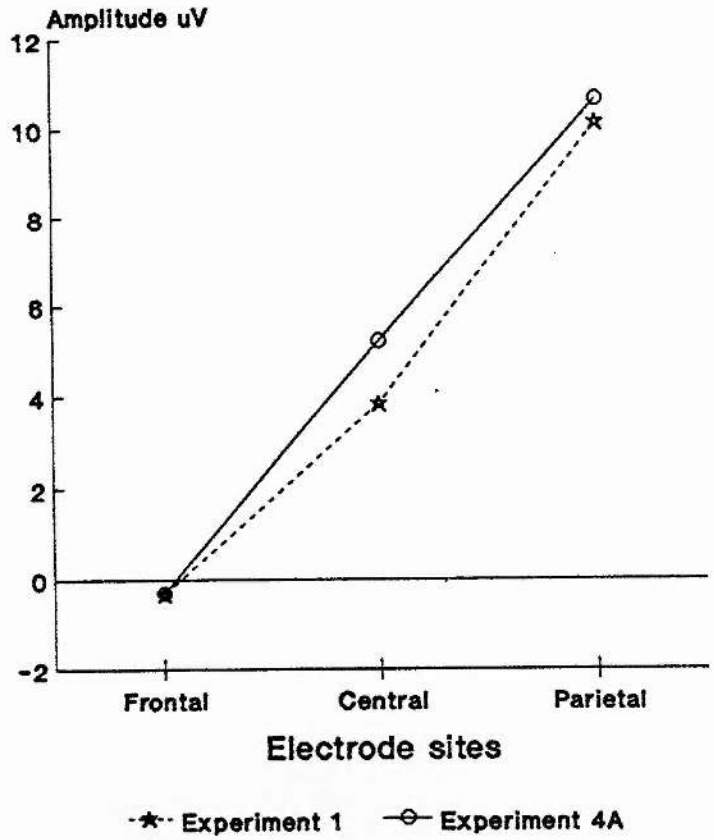


Figure 7.6a Graph illustrating the amplitude of the P300 deflection elicited by targets at each electrode site (collapsed over chain) for experiment 1 and experiment 4a.

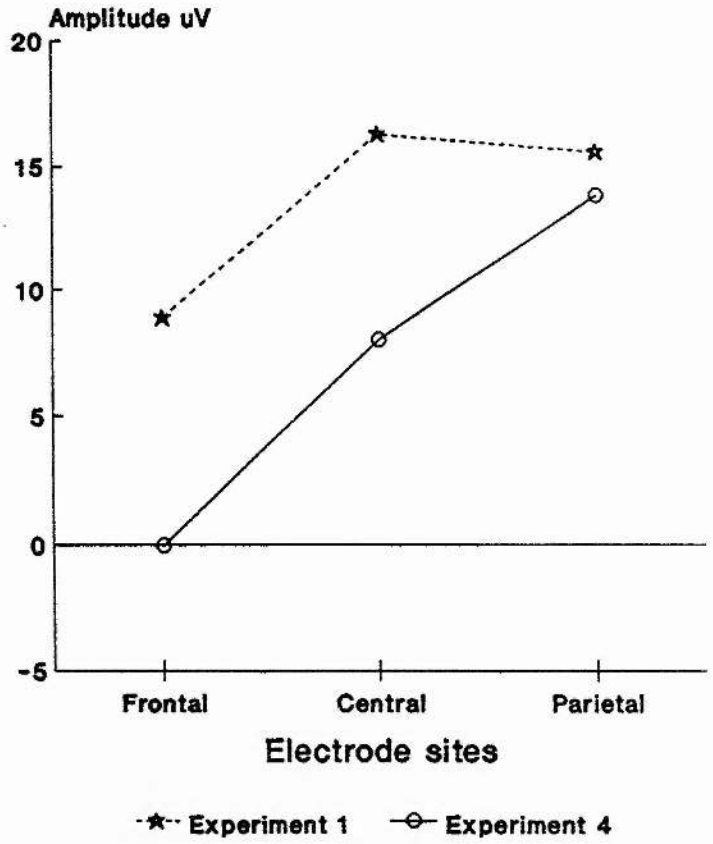


Figure 7.6b Graph illustrating the amplitude of the P300 deflection elicited by rare nontargets at each electrode site (collapsed over chain) for experiment 1 and experiment 4a.

scalp distribution of the P300 deflection elicited by novel sounds in the two experiments may be due to an absence of an anterior positivity in the second experiment.

N100

ANOVA comparing the N100 data of experiment 1 and experiment 4 before and after rescaling showed no significant effect of experiment and no significant interactions with experiment.

P170

The ANOVA comparing the P170 elicited by targets and rare deviant nontargets in the two experiments showed a significant experiment by condition by chain interaction ($F(1.9,41.7)=5.401$, $P<0.01$) which remained in the analysis of the rescaled data ($F(1.8,40.5)=3.447$, $P<0.05$). The interaction was obtained because in Experiment 1 both the target tones and rare nontarget novel sounds produced a P170 which did not differ significantly in amplitude between electrode chains. In contrast, in the present experiment the P170 elicited by targets showed no difference in amplitude across electrode chains but that elicited by the rare novel sounds was of maximum amplitude at the midline.

A significant experiment by condition by site interaction was obtained ($F(1.4,31.2)=4.914$, $P<0.05$) which remained in the analysis of the rescaled data ($F(1.4,30.0)=6.560$, $P=0.01$). This was obtained because in both experiments the P170 elicited by the target tones had a parietal maximum, whereas that elicited by

the rare nontarget novel sounds was of maximum amplitude at frontal sites in experiment 1 but had a central maximum in the present experiment.

500-900 ms region

An ANOVA, comparing the amplitude of the 500-900 ms region of the waveforms elicited by the targets and rare nontarget novel sounds in Experiment 1 and the present experiment, showed that this region of the waveform elicited by both categories of rare stimuli in the present experiment was more negative than that elicited by the rare stimuli in Experiment 1. There was a greater difference in amplitude between the two experiments at frontal than central or parietal sites and a greater difference at central than parietal sites (experiment by site interaction $F(1.1,24.7)=5.361$, $P<0.05$). A significant experiment by chain by site interaction ($F(2.0,43.9)=4.188$, $P<0.05$) was produced because although the difference in amplitude of the 500-900 ms region differed across site at midline and left hemisphere sites it did not differ at right hemisphere sites.

Summary of Results

In the present experiment, the target tones and novel sounds elicited P300 deflections which did not differ significantly in latency. The P300 deflection elicited by the novel sounds had a midline maximum, whereas the targets elicited a P300 deflection which was evenly distributed across electrode chains. The between experiment ANOVA, however, showed this difference in distribution to be more marked in experiment 1. In the present experiment, the P300 deflection elicited by both categories of rare stimuli had a parietal maximum. In contrast, in experiment 1 the novel sounds elicited a centro-parietally distributed P300 deflection and the

targets a parietally distributed deflection. The between experiment ANOVA comparing the amplitude of the P300 elicited by the novel sound in experiment 1 and the present experiment showed a decrease in amplitude between the two experiments at frontal and central sites. This suggests that the change of the P300 deflection elicited by the novel sounds from a fronto-central to a parietal scalp distribution between the two experiments is due to a change in positivity at anterior sites.

An N100 deflection with a midline central maximum was elicited by both categories of rare stimuli. No significant differences in N100 were found between experiment 1 and the present experiment.

The P170 elicited by the novel sounds was more positive than that elicited by the targets. Unlike experiment 1, where the P170 elicited by both categories of rare stimuli was distributed evenly over the three electrode chains, in the present experiment the P170 elicited by the novel sounds had a midline maximum. The P170 elicited by the targets had a parietal maximum in both experiments, whereas that elicited by the novel sounds had a frontal maximum in experiment 1 but a central maximum in the present experiment.

The amplitude of the N200 region did not differ significantly between the two rare conditions. The N200 region was found to be more positive over central and parietal sites than over frontal sites, probably due to the influence of the P300.

The region of waveform elicited by the targets between 500-900 ms was significantly more positive than the same region elicited by the novel sounds. At parietal sites this difference was larger at the midline than laterally but at frontal and

central sites there were no significant differences between chains. Over the midline and left hemisphere the 500-900 ms region had maximum positivity over parietal sites for both categories of rare stimuli, over the right hemisphere maximum positivity was over centro-parietal sites.

EXPERIMENT 4B

METHOD

Subjects

18 subjects were tested (mean age 29, range 21-39 yrs, 9 female). All subjects were paid volunteers.

Design

Subjects performed two tasks. In task (i) subjects were presented with one of the stimulus sequences from Experiment 1 which consisted of the random mixing of frequent high tones (P=0.70), target tones (P=0.15) and rare novel sounds (P=0.15). In task (ii) subjects were presented with the stimulus sequence used in Experiment 4A which was the same sequence as presented in task (i) but with the frequent stimuli omitted. Task (i) will be referred to as the 'frequents present task' whereas task (ii) will be referred to as the 'omitted frequents task'. The order of presentation of the two tasks was counterbalanced across subjects.

Procedure

For task (i) and task (ii) the same practice sequences and instructions were given as for Experiment 1 and Experiment 4A respectively. For each task a button press was required in response to the target tones. The presentation of the stimulus sequences was exactly as in the corresponding preceding experiments. A break of approximately 2-3 minutes was given between each task.

DATA ANALYSIS

The waveforms averaged over the 18 subjects for the two conditions in task (i) are shown in Figure 7.7a and those for task (ii) are shown in Figure 7.7b.

Separate averages were obtained for each experimental condition. In task (i) the waveform in response to the frequents was averaged over a mean of 170 trials (range 124-210), that in response to the target was averaged over a mean of 40 trials (range 32-45) and that in response to the rare nontarget novel sounds was averaged over a mean of 37 trials (range 29-45). In task (ii) the waveform in response to the targets was averaged over a mean of 40 trials (range 29-45) and that in response to the rare deviant sounds was averaged over a mean of 38 trials (range 23-44).

Amplitude and latency values for the peaks were obtained as described for experiment 1 and experiment 4a.

An 18*2*2*3*3 (subject*task*condition*chain*site) ANOVA was performed for the P300, N100, P170, N200 and 500-900 ms region comparing the response elicited

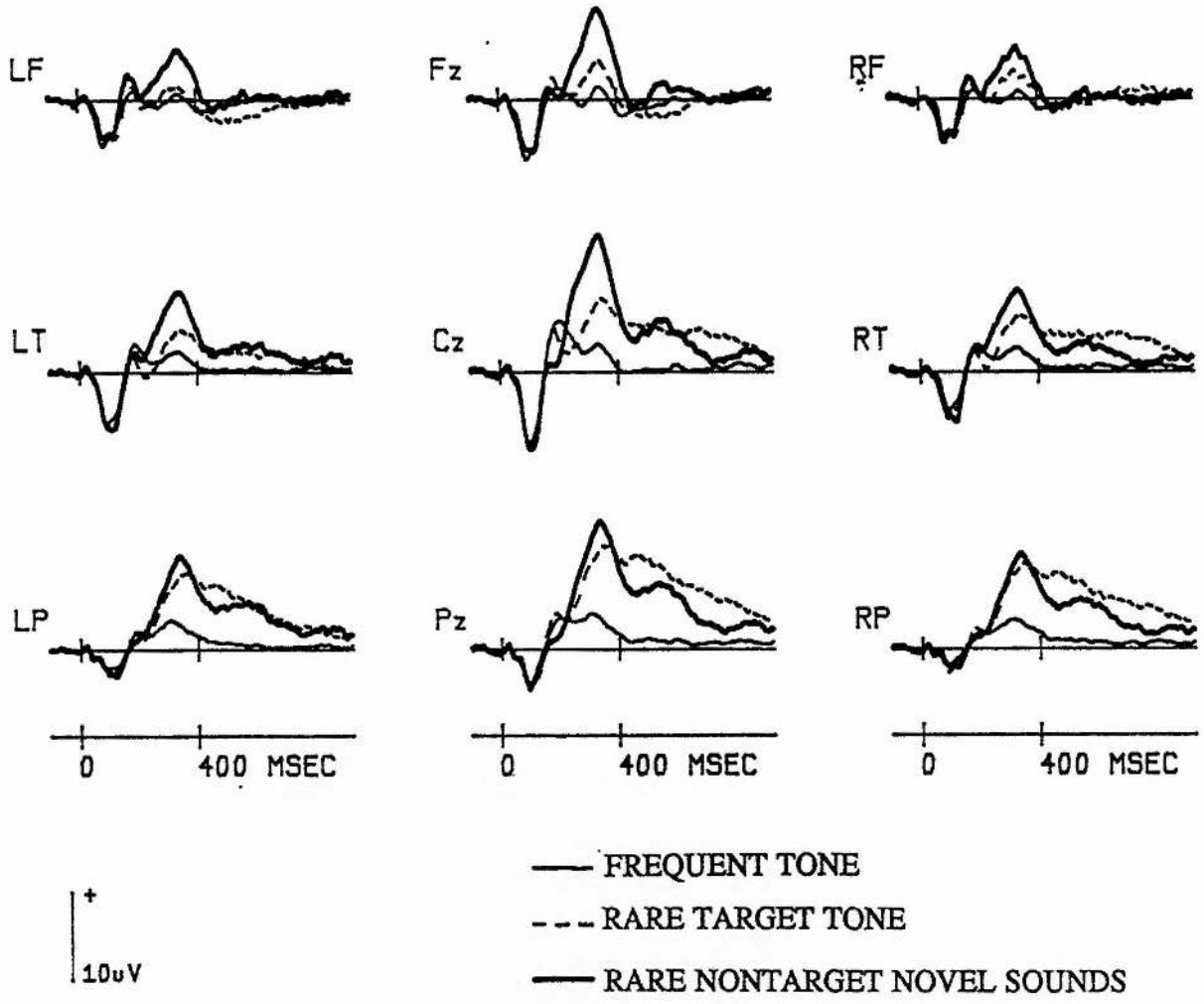


Figure 7.7a Waveform averaged over 18 subjects for the two conditions in task (i) ('frequents present' task) of experiment 4b.

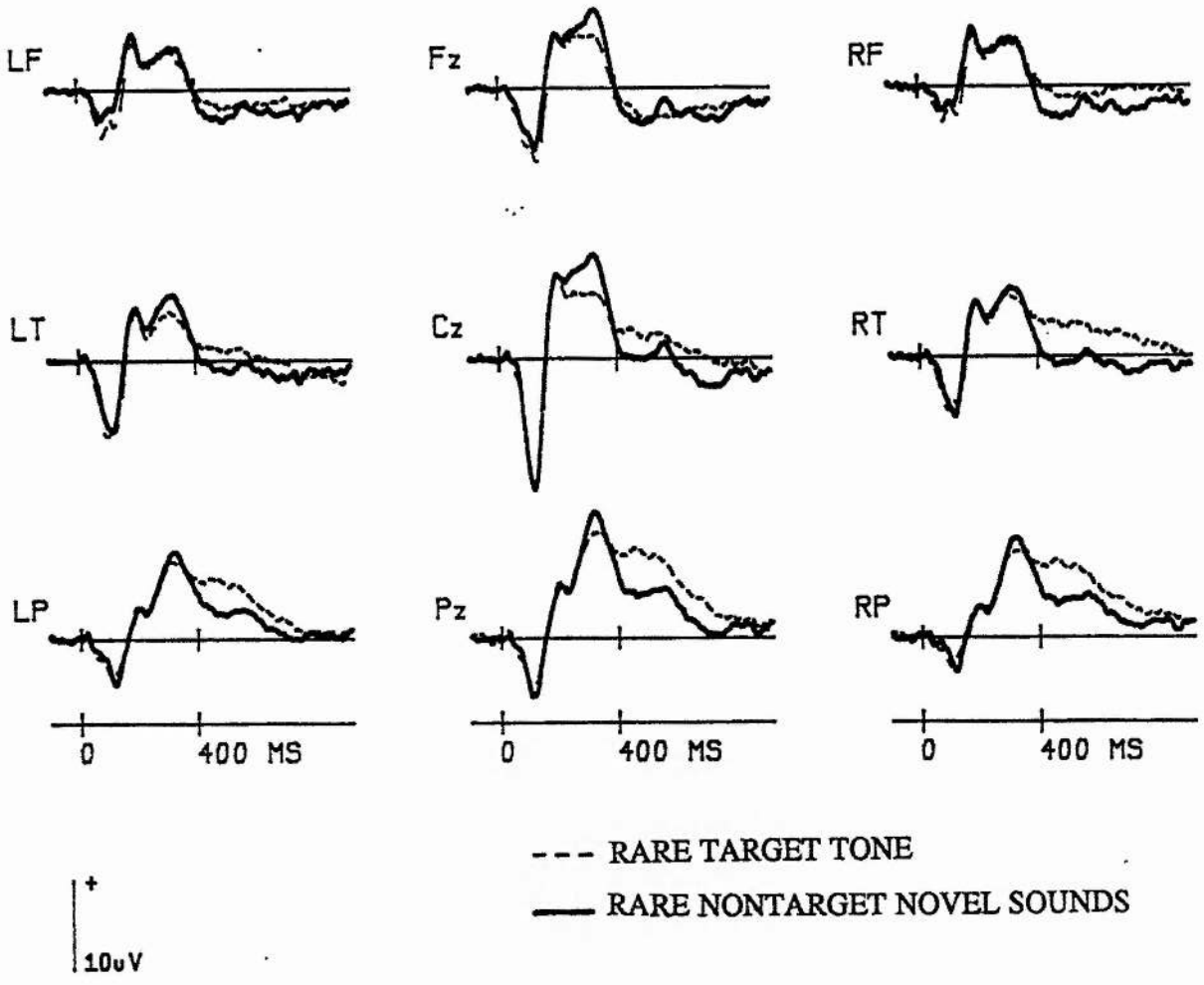


Figure 7.7b Waveform averaged over 18 subjects for the two conditions in task (ii) ('omitted frequents' task) of experiment 4b.

Table 7.8. Mean latency of the P300 deflection, elicited by target tones and rare novel sounds at Cz and Pz electrode sites, in the 'frequents present' and 'omitted frequents' tasks of Experiment 4b.

		'FREQUENTS PRESENT'		'OMITTED FREQUENTS'	
		CZ	PZ	CZ	PZ
Target tones	Mean	340.0	351.5	329.0	332.8
	SD	17.5	32.7	18.8	27.3
Novel sounds	Mean	325.7	336.0	326.2	327.6
	SD	16.7	21.9	19.2	15.5

Table 7.9. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli in the 'frequents present' task, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,17	18.59	0.000*	Condition (CC)	1,17	0.01	0.906
Chain (CH)	2.0,33.8	56.90	0.000*	Chain (CH)	2.0,33.8	57.06	0.000*
Site (ST)	1.2,20.5	32.67	0.000*	Site (ST)	1.2,20.6	32.14	0.000*
CC*CH	1.7,29.5	17.37	0.000*	CC*CH	1.8,29.8	19.50	0.000*
CC*ST	1.5,25.8	14.92	0.000*	CC*ST	1.5,25.6	12.17	0.001*
CH*ST	3.0,51.6	3.80	0.015*	CH*ST	3.0,51.6	3.91	0.013*
CC*CH*ST	3.2,53.6	4.85	0.004*	CC*CH*ST	3.2,54.3	5.06	0.003*

* indicates statistical significance at the 0.05 level or better

Table 7.10. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli in the 'omitted frequents' task , before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,17	3.35	0.085	Condition (CC)	1,17	0.32	0.577
Chain (CH)	1.8,31.1	30.66	0.000*	Chain (CH)	1.8,31.0	30.18	0.000*
Site (ST)	1.2,20.3	16.71	0.000*	Site (ST)	1.2,20.3	16.78	0.000*
CC*CH	1.8,30.0	7.13	0.004*	CC*CH	1.7,29.4	4.95	0.018*
CC*ST	1.5,25.0	1.70	0.206	CC*ST	1.5,25.5	2.08	0.156
CH*ST	2.7,46.7	1.36	0.268	CH*ST	2.8,47.0	1.39	0.259
CC*CH*ST	3.0,50.3	5.64	0.002*	CC*CH*ST	3.0,51.5	5.78	0.002*

* indicates statistical significance at the 0.05 level or better

by the targets and the deviant sounds in the two tasks. In addition, an 18*2*3*3 (subject*condition*chain*site) ANOVA was performed for each task comparing the P300 elicited by the targets and the rare nontarget novel sounds. These ANOVAs were performed on the data both before and after rescaling.

RESULTS

P300 peak latency

The latencies of the P3 elicited by the targets and the novel sounds in the two tasks are shown in Table 7.8. The peak latency was found to be significantly earlier at Cz than at Pz for both conditions. A significant effect of site was obtained ($F(1,17)=4.674$, $P<0.05$). The P3 elicited by the novel sounds was significantly earlier than that elicited by the target tones in both tasks ($F(1,17)=4.966$, $P<0.05$) but the difference in latency between the two conditions was significantly greater in the 'frequents present' task than in the 'omitted frequents' task producing a significant task by condition interaction ($F(1,17)=6.368$, $P<0.05$).

P300 amplitude

Task (i), 'frequents present'

As shown in Table 7.9, the results of the ANOVA are very similar to those obtained in Experiment 1. The P300 elicited by the novel sounds was significantly larger in amplitude than that elicited by the target tones.

A significant condition by chain by site interaction was obtained before and after rescaling. As in Experiment 1, this was obtained because the P3b elicited by the target tones was maximally distributed over parietal sites for all electrode chains, whereas the P3a elicited by the novel sounds had a centro-parietal maximum at the midline but a parietal maximum at lateral sites.

Task (ii), 'omitted frequents'

The results of the analysis, shown in Table 7.10, are very similar to those obtained for Experiment 4A.

The P300 elicited by the targets and the novel sounds did not differ significantly in amplitude between the two conditions.

Table 7.10 shows that a significant condition by chain interaction was obtained before and after rescaling. Newman Keuls testing showed that the P300 elicited by both the targets and novel sounds was significantly larger at midline than at lateral sites which did not differ. Inspection of the mean amplitudes in each condition suggests that the interaction results from the difference in amplitude between midline and lateral sites being larger for the P300 elicited by the novel sounds than for that elicited by the targets.

A significant main effect of site was obtained which remained in the analysis of the rescaled data. Newman Keuls testing showed that the P300 was significantly larger at parietal than central and frontal sites and significantly larger at central than at frontal sites. Unlike the 'frequents present' task, no significant condition by site interaction was obtained in the omitted frequents task.

A significant interaction was obtained between condition, chain and site which remained in the analysis of the rescaled data. Newman Keuls testing showed that the P300 deflection elicited by the novel sounds did not differ significantly in amplitude between electrode chain at frontal sites but was significantly larger at midline than at lateral sites at central and parietal sites. For the P300 elicited by the targets no significant difference in amplitude was found between electrode chains at frontal and central sites but at parietal sites the P300 deflection was significantly larger at the midline than at left hemisphere sites but no significant differences in P300 amplitude were found between the midline and the right hemisphere or the right and left hemispheres.

Comparison of P300 elicited in Task (i) and Task (ii)

As shown in Table 7.11, no significant main effect of task was obtained.

A significant task by condition by site interaction was obtained before and after rescaling. The interaction was due to the P300 being parietally distributed in response to both the targets and deviant sounds in the 'omitted frequents' task but having a parietal maximum in response to the targets and a centro-parietal maximum in response to the deviant sounds in the 'frequents present' task. This is shown in Figures 7.8a and 7.8b.

A significant task by chain by site interaction was obtained which remained in the analysis of the rescaled data, this is shown in Figure 7.9a and 7.9b. Newman Keuls testing showed that in the 'frequents present' task, the P300 deflection elicited by both categories of stimuli at midline sites did not differ significantly in amplitude

Table 7.11. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli in the 'frequents present' task and 'omitted frequents' task, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,17	0.71	0.408
Condition (CC)	1,17	12.11	0.003*
Chain (CH)	1.9,32.3	48.48	0.000*
Site (ST)	1.2,20.2	24.59	0.000*
TA*CC	1,17	4.75	0.044*
TA*CH	1.9,32.8	2.45	0.104
TA*ST	1.3,22.1	4.94	0.029*
CC*CH	1.6,27.8	18.40	0.000*
CC*ST	1.4,23.3	6.12	0.014*
CH*ST	3.0,51.4	2.01	0.124
TA*CC*CH	1.8,30.5	2.32	0.121
TA*CC*ST	1.7,28.5	10.75	0.001*
TA*CH*ST	2.5,42.8	3.29	0.037*
CC*CH*ST	2.9,49.5	7.68	0.000*
TA*CC*CH*ST	3.2,54.9	0.92	0.439

RESCALED AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,17	0.50	0.486
Condition (CC)	1,17	0.10	0.759
Chain (CH)	1.9,32.3	47.28	0.000*
Site (ST)	1.2,20.2	24.05	0.000*
TA*CC	1,17	0.51	0.482
TA*CH	1.9,32.4	1.45	0.251
TA*ST	1.3,21.7	4.38	0.040*
CC*CH	1.6,27.5	17.90	0.000*
CC*ST	1.4,23.3	6.30	0.013*
CH*ST	3.0,51.2	1.96	0.132
TA*CC*CH	1.8,30.7	3.25	0.057
TA*CC*ST	1.8,30.8	4.01	0.032*
TA*CH*ST	2.5,43.0	3.21	0.040*
CC*CH*ST	2.9,49.4	7.94	0.000*
CC*CH*ST	3.3,56.0	1.09	0.366

* indicates statistical significance at the 0.05 level or better

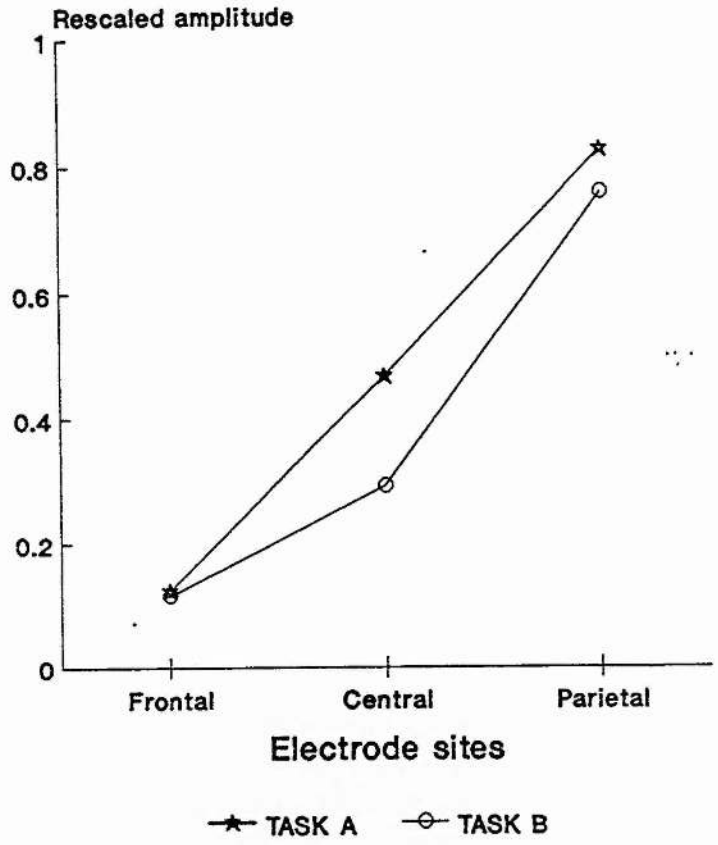


Figure 7.8a Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by targets in the 'frequents present' task and the 'omitted frequents' task of experiment 4b.

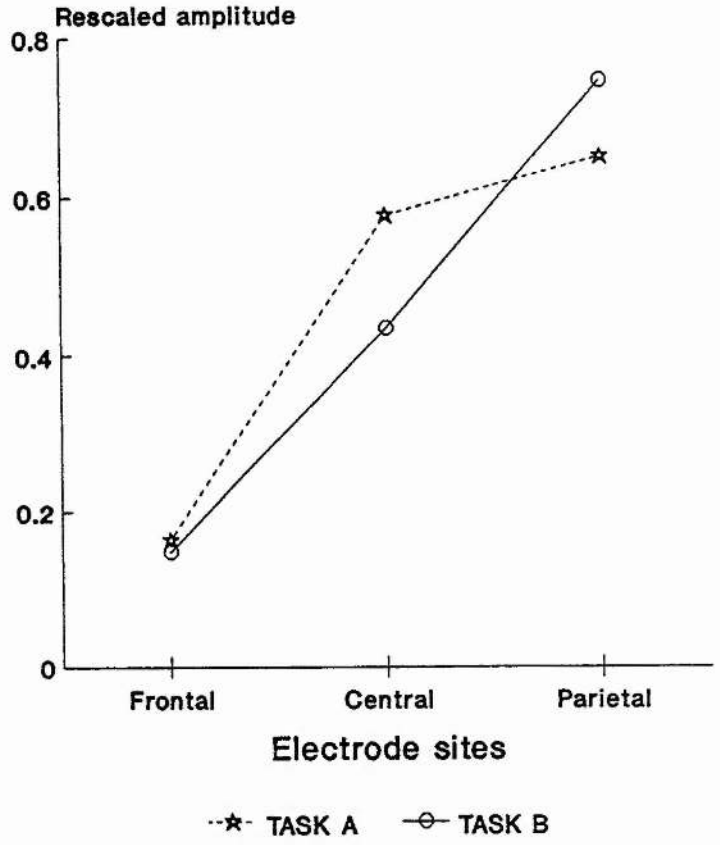


Figure 7.8b Graph illustrating the distribution, across site, of rescaled amplitude of the P300 deflection elicited by rare nontargets in the 'frequents present' task and 'omitted frequents' task of experiment 4b.

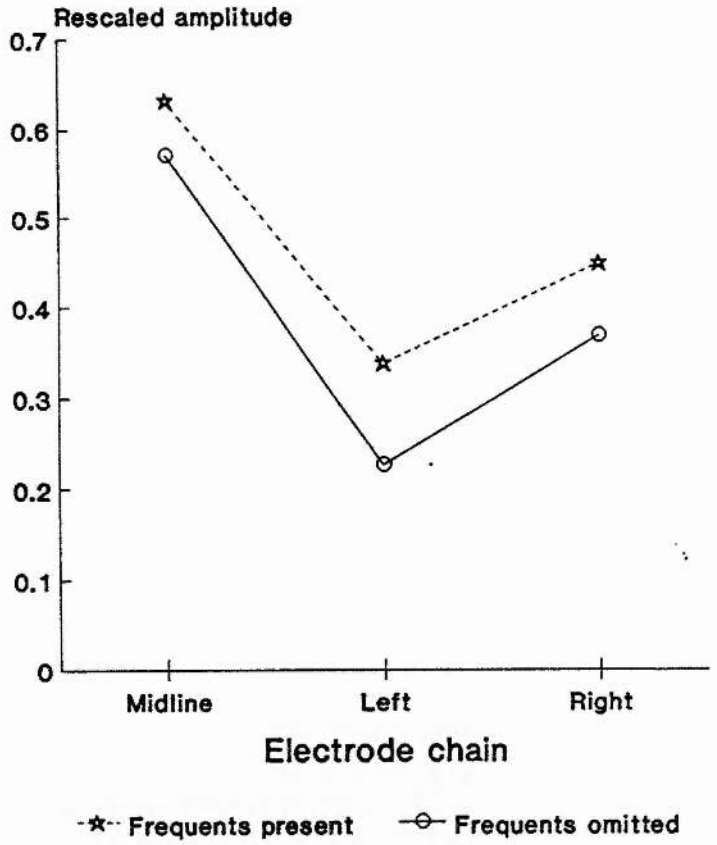


Figure 7.9a Graph illustrating the distribution, across electrode chain, of rescaled amplitude of the P300 deflection elicited by targets in the 'frequents present' task and the 'omitted frequents' task of experiment 4b.

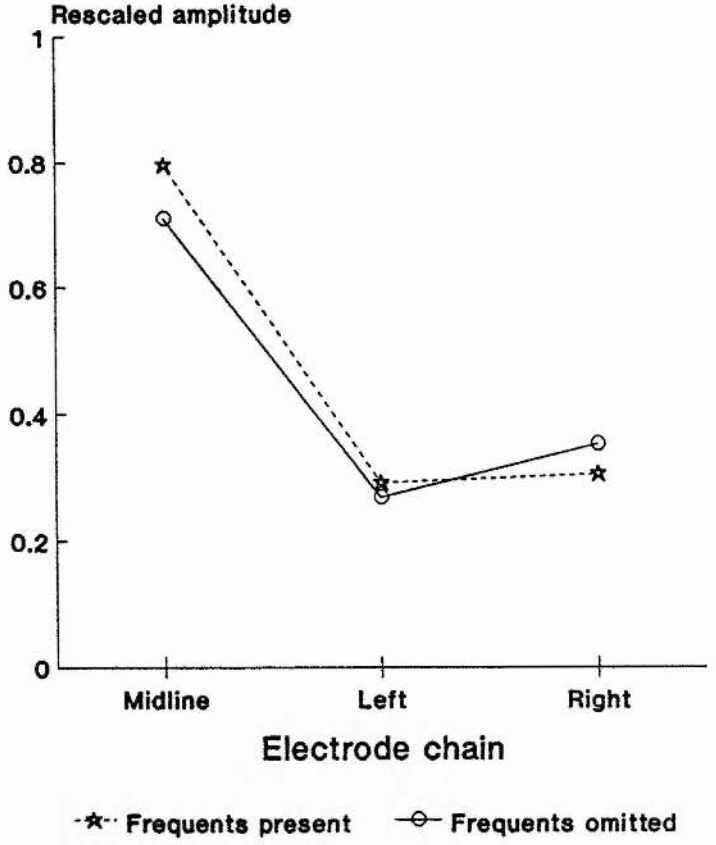


Figure 7.9b Graph illustrating the distribution, across electrode chain, of rescaled amplitude of the P300 deflection elicited by rare nontargets in the 'frequents present' task and 'omitted frequents' task of experiment 4b.

between parietal and central sites but was significantly larger at both than at frontal sites. In contrast, the P300 deflection elicited by both categories of rare stimuli over both right and left hemispheres was significantly larger at parietal than at frontal sites but did not differ significantly between parietal and temporal or temporal and frontal sites. In the 'omitted frequents' task, the P300 deflection elicited by both categories of rare stimuli at all three electrode chains was significantly larger at parietal than frontal sites but showed no significant difference between central and frontal or central and parietal sites.

N100

The N100 elicited by the targets had a mean latency at Cz of 102 ms in the 'frequents present' task and 112.7 ms in the 'omitted frequents' task, the N100 elicited by the novel sounds had a mean latency at Cz of 106.6 ms in the 'frequents present' task and 111 ms in the 'omitted frequents' task. No significant effects of task ($F(1,17)=2.207$, $P>0.05$) or condition ($F(1,17)=1.083$, $P>0.05$) nor interaction between task and condition ($F(1,17)=2.28$, $P>0.05$) were found on N100 latency.

The results of the ANOVA investigating the amplitude of the N100 are shown in Table 7.12 of Appendix. A significant main effect of task was obtained because the N100 elicited in the 'omitted frequents' task was more negative than that elicited in the 'frequents present' task.

Table 7.12 of Appendix shows that a significant task by chain by site interaction was obtained before and after rescaling. In both tasks the N100 at the midline was more negative than that elicited at lateral sites. The interaction was obtained because in the 'frequents present' task the difference between midline and left lateral sites did

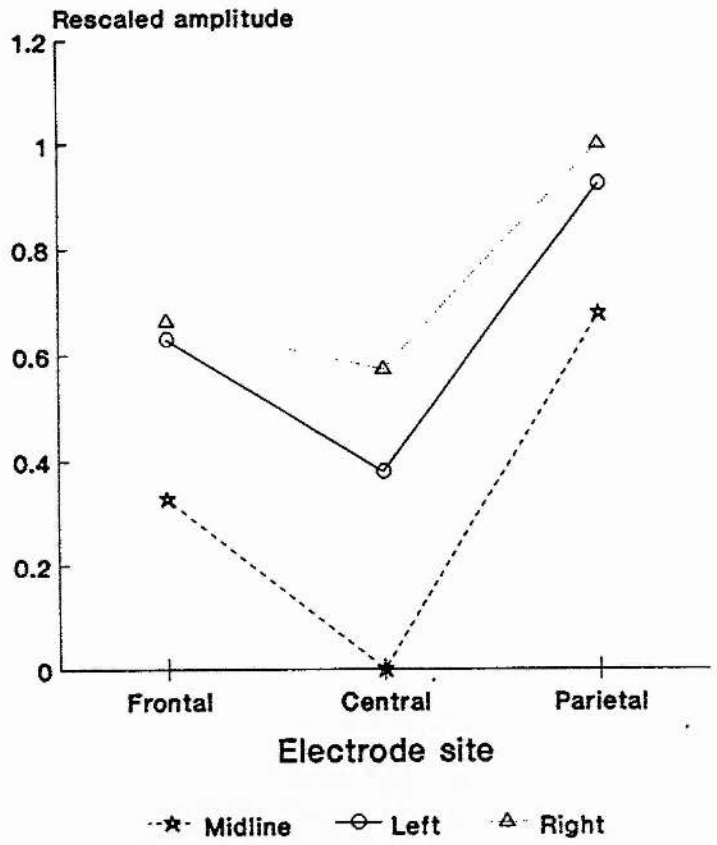


Figure 7.10a Graph illustrating the distribution, across site, of rescaled amplitude of the N100 deflection elicited over each electrode chain for the 'frequents present' task (collapsed over condition).

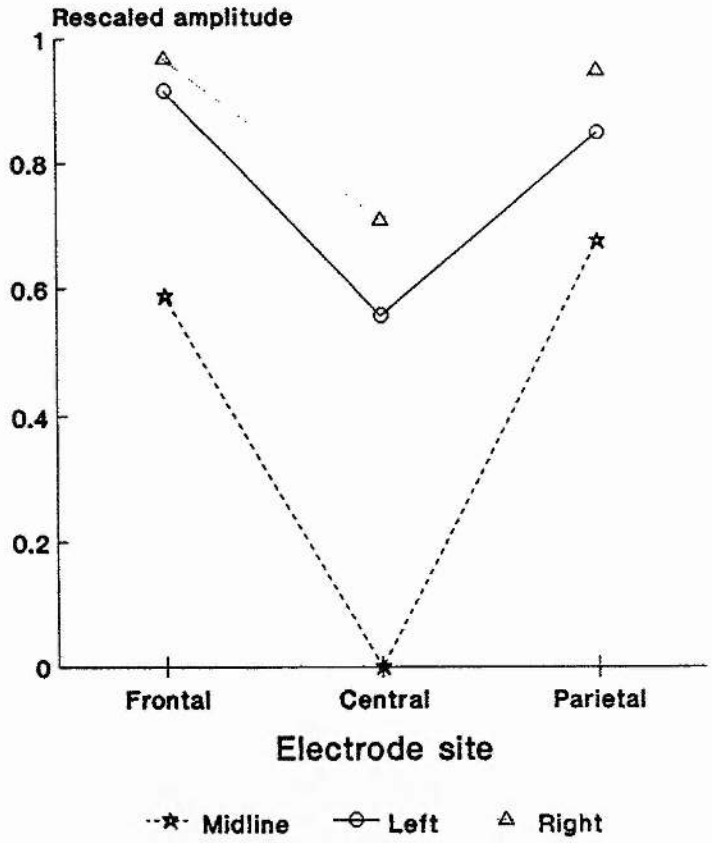


Figure 7.10b Graph illustrating the distribution, across site, of rescaled amplitude of the N100 deflection elicited over each electrode chain for the 'omitted frequents' task (collapsed over condition).

not differ significantly between sites. In contrast, the difference between midline and right hemisphere sites was larger at central than frontal and parietal sites. In the 'omitted frequents' task the differences between midline and left, and midline and right, hemisphere sites were significantly larger at central and frontal sites than at parietal sites. The scalp distribution indicated by the rescaled data suggested that the N100 had a central maximum in the 'omitted frequents' task which was more marked at midline than lateral sites but a fronto-central distribution in the 'frequents present' task for all electrode chains (see Figures 7.10a and 7.10b).

P170

The P170 elicited by the targets had a mean latency at Fz of 184 ms in the 'frequents present' task and 193.7 ms in the 'omitted frequents' task, the P170 elicited by the novel sounds had a mean latency at Fz of 177.6 ms in the 'frequents present' task and 187.8 ms in the 'omitted frequents' task. No significant main effect of task ($F(1,17)=1.706$, $P>0.05$) nor task by condition interaction ($F(1,17)=0.025$, $P>0.05$) were found but for both tasks the P170 elicited by the targets was found to have a longer latency than that elicited by the novel sounds ($F(1,17)=7.38$, $P<0.05$).

The results of the ANOVA on the P170 amplitude data are given in Table 7.13 of Appendix. It can be seen that the P170 is significantly more positive in the 'omitted frequents' task than in the 'frequents present' task.

A significant task by condition by chain interaction was obtained before and after rescaling. Post hoc tests showed that the P170 elicited by the novel sounds differed in amplitude from the 'frequents present' task to the 'omitted frequents' task to a

greater extent than that elicited by the targets and that this difference was significantly larger at midline than at lateral sites.

A significant task by chain by site interaction was obtained before and after rescaling. This was obtained because in both tasks, the P170 was more positive over frontal than over central and parietal sites for both lateral chains. At midline sites the P170 elicited in the 'frequents present' task had a centro-parietal maximum, whereas that elicited in the 'omitted frequents' task had a central maximum.

500-900 ms region

The results of the ANOVA are given in Table 7.14 of Appendix. It can be seen that a significant interaction was obtained between task and chain before and after rescaling. This was obtained because in the 'frequents present' task the 500-900 ms region did not differ between midline and right hemisphere sites or right and left hemisphere sites but was significantly more positive over the midline than over left hemisphere sites. In contrast, in the 'omitted frequents' task no significant differences in the 500-900 ms region were found between midline and lateral sites but this region was found to be significantly more positive over right than left hemisphere sites.

A significant task by site interaction was obtained before and after rescaling. The 500-900 ms region was more negative in the 'omitted frequents' task than in the 'frequents present' task. The interaction was obtained because the difference in the amplitude of the 500-900 ms region between the two tasks was significantly greater at central than at frontal and parietal sites.

Table 7.15. Mean reaction time (ms) to respond to target tone, mean number of hits, mean number of false alarms and corresponding standard deviations (SD) in the auditory oddball tasks of experiment 4B.

		MEAN	SD
Reaction time	TASK (i)	496.6	110.1
	TASK (ii)	478.8	130.1
Hits	TASK (i)	44.3	0.9
	TASK (ii)	44.8	0.4
False alarms	TASK (i)	0.8	0.6
	TASK (ii)	0.8	1.5

No significant interactions were found involving task and condition.

Behavioural data

The mean reaction times for the button press response to the target stimuli, the mean number of hits and false alarms are given in Table 7.15.

Summary of Results

In both tasks, the novel sounds elicited a P300 deflection with a significantly earlier latency than that elicited by the target tones. This latency difference was larger in the 'frequents present' task than in the 'omitted frequents' task. In the 'frequents present' task, the P300 deflection elicited by the targets had a parietal maximum, whereas that elicited by the novel sounds had a centro-parietal maximum. In the 'omitted frequents' task, both categories of rare stimuli elicited a P300 deflection with a parietal maximum.

The latency of the N100 deflection did not differ significantly between the two tasks. The N100 deflection elicited by both categories of rare stimuli was more negative in the 'omitted frequents' task than in the 'frequents present' task. In both tasks, the N100 elicited by both categories of rare stimuli was more negative at the midline than at lateral sites. In the 'omitted frequents' task, the differences between midline and lateral chains were larger at frontal and central sites, whereas in the 'frequents present' task, this was only true for the difference between midline and right hemisphere sites. In the 'frequents present' task, the N100 had a fronto-central maximum, whereas in the 'omitted frequents' task the N100 was maximally distributed over central sites.

In both tasks, the P170 elicited by the targets had a longer latency than that elicited by the novel sounds. The P170 was significantly more positive in the 'omitted frequents' than in the 'frequents present' task. This amplitude difference was larger at midline than at lateral sites and was larger for novel sounds than targets. For both tasks, the P170 was significantly more positive over lateral frontal sites than over central and parietal sites. At the midline the P170 had a centro-parietal maximum in the 'frequents present' task but a central maximum in the 'omitted frequents' task.

The 500-900 ms region was more negative in the 'omitted frequents' task than in the 'frequents present' task. This amplitude difference was larger at central than frontal and parietal sites.

DISCUSSION

P300

The hypothesis proposed in the Introduction is partly supported by the results of the present experiment. It was found that, when the frequent stimuli were omitted from the task, a P3a (defined as a P300 deflection with a centro-parietal maximum) was not elicited by the rare novel sounds. The P3b elicited by the target tones, however, was unaffected by frequent stimulus omission. In addition, a P3 deflection with a parietal maximum, similar to the P3b, was elicited by the rare novel sounds when the frequent stimuli were not present in the task. The results therefore suggest that detection of a mismatch, between a representation of the features of the frequently occurring stimulus and those of the presented stimulus, is necessary for the

elicitation of the P3a. The detection of a mismatch, however, is not necessary for the elicitation of the P3b by target stimuli nor for the elicitation of a parietally distributed P300 by the novel sounds.

The results are consistent with Naatanen's (1990) proposal that mismatch detection is a necessary precursor of the P3a component thought to indicate a switch to processing whose results are available for conscious report. The results of the present experiment suggest that this is not the only route available to attentional processing in a one channel oddball task. The parietally distributed P3b component elicited by targets is thought to reflect further processing of task relevant stimuli following their discrimination and categorisation by attentional processing. The parietally distributed P300 elicited by the novel sounds did not differ significantly in scalp distribution from that elicited by the target tones, suggesting that the same neuronal generator(s) was activated by both stimuli. In the present experiment, therefore, it is suggested that both the target tones and novel sounds gained access to attentional processing. It is possible that access to attentional processing may have been achieved by a template matching process, whereby the incoming stimulus was compared with an attentionally maintained template of the task relevant stimulus/stimuli.

The task used in the present experiment was a go/nogo task in which the subject made a button press response to the target tone and withheld this response to the novel sounds. The go/no-go studies discussed in Experiment 3 reported the elicitation of a centro-parietally distributed P300 in response to no-go stimuli but a parietally distributed P300 in response to go stimuli. In the present experiment, however, both categories of stimuli elicited a P300 with a parietal maximum. The difference in the distribution of the P300 elicited by no-go stimuli in the present

oddball experiments and the previously reported go/no-go studies could be due to the difference in design of the two tasks. In the go/no-go tasks the category of stimulus (go/no-go) is unpredictable but the temporal interval between the task relevant stimuli is predictable. In the oddball experiments both the stimulus category and the temporal interval between the task relevant stimuli are unpredictable. The difference in temporal predictability of the two task relevant stimuli in the go/no-go and the oddball tasks may affect the nature of the further processing of the no-go stimuli in the two situations.

The results suggest that the centro-parietally distributed P300 deflection elicited by the novel sounds in Experiment 1 and the more posteriorly distributed (parieto-central) P300 deflection elicited in Experiment 3 were not produced by the activation of a "no-go" generator. The results are more consistent with the view that the centro-parietal distribution of the P3a elicited by the novel sounds was produced because of a contribution to the waveform of anteriorly distributed activity resulting from the passive mismatch detection process proposed by Naatanen (1990). It is suggested that in the three stimulus oddball task used in experiments 1 and 2, only the novel sounds differed sufficiently from the frequents to elicit this anterior activity. In contrast, it is suggested that both the target tones and the rare novel sounds cause the activation of the more posterior generator since both stimuli are task relevant.

The results of the present study provide further information concerning subjective probability and the elicitation of the P3b. The amplitude of the P3b elicited by target stimuli has been found to be related to subjective probability. Larger amplitude P3bs are produced in response to more improbable stimuli (e.g. Tueting et al., 1971; Duncan-Johnson and Donchin, 1977). Two types of subjective probability

can be distinguished: one is 'sequential probability', the probability of the target stimulus within a sequence of stimuli, and the other is 'temporal probability', the probability of a target stimulus within a period of time (Fitzgerald and Picton, 1981). Ford et al. (1976) suggested that the effect of stimulus uncertainty on the P3b may be due to temporal uncertainty rather than sequential uncertainty. A number of studies specifically carried out to unconfound the effect of these two types of probability have found that temporal probability determines the amplitude of the P3b (e.g. Fitzgerald and Picton, 1981; Scott et al., 1989). The importance of temporal uncertainty is supported by the finding in the present experiment that the target P3b is unaffected by the omission of the frequent stimuli. When the frequent stimuli were omitted the sequential probability increased from 0.15 to 0.5 but no change in the amplitude or distribution of the target P3b was found.

N100

No difference in the N100 was found between Experiment 1 and Experiment 4A. When the two tasks were performed by the same group of subjects, however, the amplitude of the N100 was larger when the frequent stimuli were omitted than when they were present in the sequence. Neurons contributing to the activity which is recorded as the N100 are thought to remain refractory for 4-5 seconds following presentation of a stimulus (Naatanen and Picton, 1987). If there is an overlap in the neurons activated by the frequent stimuli and both categories of rare stimuli, the neurons activated by the frequents will still be in a refractory state when the rare stimuli are presented. The N100 elicited by both categories of rare stimuli will therefore be of smaller amplitude than that elicited when the frequent stimuli are omitted. When the frequent stimuli are omitted the gap between stimuli is long enough for the neurons to have recovered from a refractory state before the next

stimulus is presented. The change in amplitude of the N100 between the two tasks may not have occurred in the between subject comparison because of variability in the amplitudes of the N100s elicited by the two groups of subjects.

P170

As in the previous experiments, the P170 elicited by the novel sounds was found to be larger in amplitude than that elicited by the target tones. It is difficult to compare the amplitude of the P170 elicited in the two tasks reported in the present experiment since the P170 was found to be superimposed on the P300 elicited by the targets and novel sounds and so amplitude measurements of the P170 were influenced by the amplitude and scalp distribution of the P300 deflection.

N200

An attempt was made to compare the N200 elicited by the targets and the novel sounds in the two tasks. A pre-stimulus baseline to peak measurement was taken. A problem with this measure was that as the N200 deflection was above the baseline on a majority of trials, this measurement did not indicate the 'size' of the deflection but how positive the peak was with respect to the pre-stimulus baseline. Alternatively a peak to peak measure could have been made, for example P170 to N200 or P300 to N200 but as both of these positive deflections differ in amplitude between conditions it would be uncertain whether changes in peak to peak amplitude would be due to changes in the strength of activity of the N200 generator or to changes in the amplitude of the positive deflections. The N200 will therefore not be discussed here.

500-900 ms region

Only small changes in the distribution of the 500-900 ms region, elicited by both categories of rare stimuli, were found between the two tasks. This is consistent with the previously discussed suggestion that the slow waves reflect the further processing of task relevant stimuli and so are dependent on the role of the stimulus in the task rather than the physical and temporal relationships between stimuli.

Summary

The results of the present experiments therefore suggest that detection of a mismatch between a stored representation of the features of the frequent stimulus and those of the presented stimulus appears to be necessary for the elicitation of the P3a but appears not to be necessary for P3b elicitation.

CHAPTER 8

EXPERIMENT 5: INVESTIGATING WHETHER DETECTION OF A MISMATCH IS SUFFICIENT FOR THE ELICITATION OF THE P3A COMPONENT

INTRODUCTION

The four experiments reported so far in this thesis present results which are consistent with Naatanen's (1990) proposal that detection of a mismatch with a sensory memory trace of the frequent stimulus is necessary for the elicitation of the P3a component of the P300 complex. This proposal is supported by the results of experiment 4 in particular, which showed that omission of the frequent stimuli from the sequence abolished the elicitation of the P3a by the rare non-target novel sounds.

The present experiment investigated whether mismatch detection, although necessary for P3a elicitation, is also sufficient for the elicitation of this component. Subjects were presented with a sequence of stimuli consisting of the random mixing of a frequently occurring novel sound, a different novel sound which occurred rarely and required a button press response (the target) and a rare non-target tone. It was proposed that a trace containing the features of the frequently occurring novel sound would be automatically formed in sensory memory. On presentation of the two categories of rare stimuli it was predicted that a comparison would be made between the features of the presented stimuli and the features held in the sensory memory trace. The rare non-target tone used in the present experiment was identical to the frequent tone presented in experiment 1 and experiment 6 and the frequent novel

sound was selected from those presented as rare non-targets in experiment 1 (Chapter 4) and was identical to that presented as a rare non-target in experiment 6 (Chapter 9). The magnitude of the mismatch between the frequent and rare non-target in the present experiment was, therefore, equivalent to that in experiments 1 and 6 in which the rare non-target novel sound elicited a P3a. It was therefore proposed that if mismatch detection is sufficient for the elicitation of the P3a, the rare non-target tones would elicit a P3a in the present experiment.

METHOD

Subjects

Twelve healthy subjects (mean age 23, range 18-26, 9 female) were tested. All were paid volunteers.

Design

Each subject was presented with one sequence of 300 stimuli. The sequence was produced by the random mixing of a frequent novel sound (P=0.70), a target novel sound (P=0.15) and a 1000 Hz tone (P=0.15). The frequent and target novel sounds were chosen to be easy to discriminate between (sounding similar to a duck quack and a thump respectively). The target novel sound required a button press response. The frequency of the non-target tone was not counterbalanced across subjects because the results of Experiment 2 showed that a rare non-target tone presented among frequent and target tones did not elicit a P3a, irrespective of frequency. If a P3a was elicited by the tone in the present experiment this would not be due,

therefore, to its frequency but would be due to its relation to other stimuli in the task. Two stimulus sequences were created for the task in which the stimuli allocated to each condition were the same but the order of stimuli differed. Presentation of the sequences was alternated between subjects.

Procedure

The experimental trials were preceded by a sequence of 15 practice trials in which the stimuli were randomly presented with the same probabilities as in the experimental sequence. The experimental trials were presented approximately 2 minutes after the completion of the practice trials. For both practice and experimental trials, the subjects were told that a sequence of sounds would be presented through the headphones which would consist predominantly of a sound similar to a duck quack with the occasional presentation of a thump or high tone. Subjects were instructed to press a button, with their preferred hand, whenever the thump was presented and not to respond in any way to the other stimuli in the sequence. Responses were to be as fast as possible while trying to avoid making mistakes. The stimulus sequence was presented as three blocks of 100 trials with a 30 s break between each block.

DATA ANALYSIS

The grand average waveform, shown in figure 8.1, was obtained by averaging together the ERPs of 12 subjects.

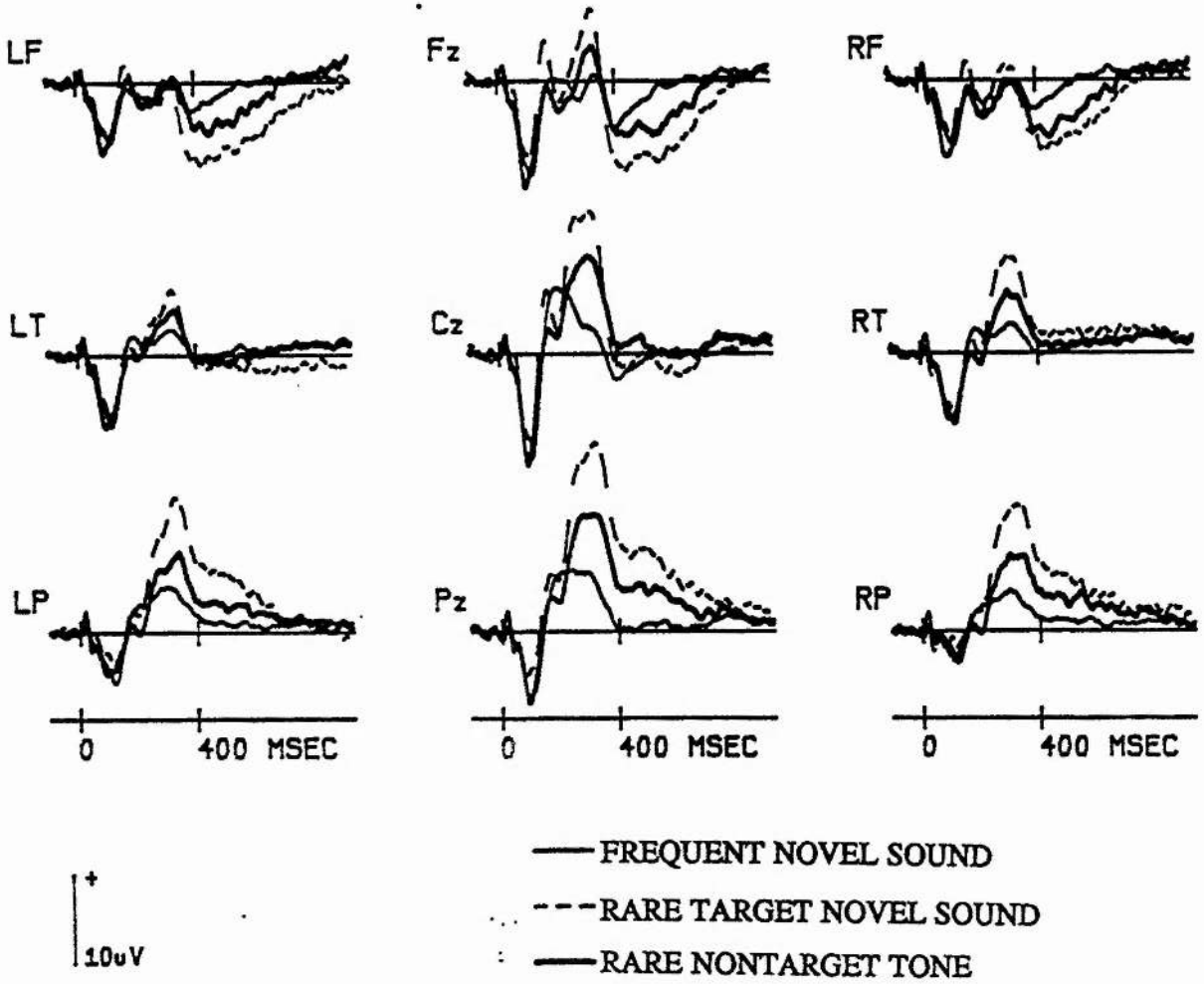


Figure 8.1 Waveforms averaged over 12 subjects for each condition of experiment 5.

The waveforms obtained in response to the frequent tones were averaged over a mean of 180 trials (range 142-205), those in response to the targets were averaged over a mean of 38 trials (range 21-45) and those in response to the rare non-targets were averaged over a mean of 38 trials (range 27-44).

The peak latencies of N100, P170 and P300, as defined in Experiment 1, were measured. The peak latency of N100 was measured at Cz in all three conditions for all subjects. In order to be consistent with the analysis of the N100 in the previous experiments reported here, the mean peak latency of the N100 elicited in the three conditions was determined for each subject. A latency window was determined for each subject which was +-12 ms round the mean latency of the N100 peak. This latency window was used for the analysis of N100 amplitude. In the previous experiments, it was only possible to measure the P170 peak in the waveforms elicited by the rare non-target stimuli. In the present experiment, however, it was possible to measure the P170 in the waveforms elicited by stimuli of all three conditions. The peak latency of P170 was therefore measured at Fz in all three conditions; this was possible for 10 of the 12 subjects. Latency windows of +-12 ms round the peak were determined for each condition, separately for each subject. For the two subjects in whose waveforms it was not possible to measure the peak, the mean peak latency of the other 10 subjects was used to determine the latency window for each condition. The peak latency of the P300 elicited by the target novel sound and the rare non-target tone was measured at Pz in 11 of the 12 subjects. As there was no significant difference in the peak latency of the P300 elicited by rare target novel sounds and rare non-target tones, the mean peak latency of the 2 conditions was used to determine the 'P300' latency window for each subject. This 'P300' latency window was used to measure the mean amplitude of the waveform in the three conditions. For the subject in whose waveform it was

impossible to measure a P300 peak elicited by either the target novel sound or non-target tone, the mean P300 peak latency obtained from the other 11 subjects was used to determine the latency window.

Repeated measures 12*3*3*3 (subject*condition*chain*site) ANOVAs were performed on the mean amplitude measures for the N100, P170 and 500-900 ms latency windows before and after the data had been rescaled. For the 'P300' latency region, separate 12*2*3*3 (subject*condition*chain*site) ANOVAs were performed comparing the P300 elicited by both the target novel sound and the rare non-target tone with the same area of the waveform elicited by the frequent stimulus. A 12*2*3*3 (subject*condition*chain*site) ANOVA was performed comparing the P300 elicited by the target novel sound and the rare non-target tone. ANOVAs investigating the 'P300' latency region were performed before and after rescaling the data.

The latency of the P300 peak elicited by the targets and rare non-targets was compared using a t-test. The latency of the N100 at Cz and the P170 at Fz, elicited by stimuli in the three conditions was investigated by a 12*3 (subject*condition) ANOVA.

RESULTS

P300

Frequent v targets

As shown in the results of the ANOVA, given in Table 8.1, the amplitude of the P300 elicited by the target novel sounds was significantly larger than that of the same area of waveform elicited by the frequent stimuli.

Table 8.1 shows a significant main effect of chain on P300 amplitude and a significant interaction which will be discussed in relation to the rescaled data.

A significant main effect of site was obtained which, as shown in Table 8.1, interacted significantly with condition. The interaction was produced because the P300 elicited by the target novel sounds was significantly larger in amplitude at parietal than at central sites and larger at central than at frontal sites. In contrast, the amplitude of the same region of the waveform elicited by the frequent novel sounds did not differ significantly between central and parietal sites but was significantly larger in amplitude at both than at frontal sites. The difference in amplitude between the P300 elicited by the targets and the same region of waveform elicited by the frequents increased from frontal to parietal sites.

Frequent v targets after rescaling

Table 8.1 shows a significant main effect of chain which interacted significantly with condition. Newman Keuls tests of rescaled amplitude across chain for each

condition showed that the P300 elicited by the target novel sound was distributed more over midline than lateral sites which did not differ. The same region of the waveform elicited by the frequent novel sound was distributed more over the midline than the left hemisphere but did not differ between the midline and right hemisphere or right and left hemisphere sites.

Table 8.1 shows a significant main effect of site but no significant interaction was found between condition and site. For both stimulus conditions, P300 amplitude was found to be larger at parietal and central sites than at frontal sites and larger at parietal than central sites (Newman Keuls comparison of amplitude across site collapsed over condition and chain).

Frequent v rare non-target

The results of the ANOVA are shown in Table 8.2. The amplitude of the P300 elicited by the rare non-target tone was significantly larger than that of the same area of waveform elicited by the frequent stimuli.

Table 8.2 shows a significant main effect of chain which interacted significantly with condition. The interaction was obtained because the P300 elicited by the rare non-target tones was larger in amplitude at midline than lateral sites which did not differ, whereas the same region of the waveform elicited by the frequent stimuli showed no difference in amplitude between chain (Newman Keuls comparison of amplitude across chain for each condition).

A significant main effect of site was obtained which interacted significantly with condition. Post hoc testing showed that, for both conditions, the amplitude of the

P300 region did not differ significantly between central and parietal sites but was significantly larger at both sites than at frontal sites. The interaction was obtained because there was a larger difference in amplitude between the P300 elicited by the rare non-target tones and the same region of waveform elicited by the frequent novel sound at the central and parietal sites than at frontal sites.

Frequent v rare non-target after rescaling

Table 8.2 shows a significant main effect of chain. For both conditions, the P300 region of waveform was distributed maximally over midline sites (Newman Keuls test of rescaled amplitude across chain collapsed over condition and site).

A significant main effect of site is shown in Table 8.2. No significant interaction was found between condition and site. Newman Keuls comparison of the amplitude of the P300 region, collapsed over condition and chain showed a parietal maximum distribution. A significant chain by site interaction was obtained. The interaction was investigated by a Newman Keuls test comparing rescaled amplitude of the P300 region, across chain, collapsed over condition, for each site. It was found that at parietal sites the P300 region was larger at midline than at lateral sites which did not differ, at central sites the P300 region was larger at midline than at left hemisphere sites but no differences were found between midline and right or right and left hemisphere sites, at frontal sites no differences were found between chains.

Table 8.1. ANOVA summary table for analysis of the amplitude of the P300 elicited by frequent and target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	70.89	0.000*	Condition (CC)	1,11	0.04	0.838
Chain (CH)	1.3,14.4	26.85	0.000*	Chain (CH)	1.6,17.3	18.37	0.000*
Site (ST)	1.3,14.3	41.21	0.000*	Site (ST)	1.4,15.2	39.98	0.000*
CC*CH	1.3,14.8	30.93	0.000*	CC*CH	2.0,21.7	6.10	0.008*
CC*ST	1.1,12.6	22.48	0.000*	CC*ST	1.3,14.8	2.72	0.113
CH*ST	2.5,27.9	0.58	0.606	CH*ST	2.7,29.9	1.14	0.346
CC*CH*ST	2.5,27.4	0.03	0.988	CC*CH*ST	2.6,28.7	1.26	0.307

* indicates statistical significance at the 0.05 level or better

Table 8.2. ANOVA summary table for analysis of the amplitude of the P300 elicited by frequent and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	6.35	0.029*	Condition (CC)	1,11	0.16	0.698
Chain (CH)	1.5,16.1	10.31	0.003*	Chain (CH)	1.6,17.9	9.88	0.002*
Site (ST)	1.7,18.2	58.48	0.000*	Site (ST)	1.6,18.1	57.95	0.000*
CC*CH	1.4,15.8	6.02	0.018*	CC*CH	1.7,18.9	2.69	0.100
CC*ST	1.2,13.3	11.06	0.004*	CC*ST	1.2,12.7	0.89	0.377
CH*ST	2.7,29.8	2.72	0.067	CH*ST	2.9,31.7	2.94	0.050*
CC*CH*ST	2.9,32.3	1.93	0.146	CC*CH*ST	3.2,35.4	2.34	0.086

* indicates statistical significance at the 0.05 level or better

Table 8.3. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Condition (CC)	1,11	64.53	0.000*
Chain (CH)	1.3,14.1	23.76	0.000*
Site (ST)	1.4,14.9	50.11	0.000*
CC*CH	1.6,17.4	13.61	0.001*
CC*ST	1.2,13.1	6.82	0.018*
CH*ST	2.2,24.6	0.79	0.477
CC*CH*ST	2.5,27.3	0.34	0.760

RESCALED AMPLITUDE			
Factors	df	F	Prob
Condition (CC)	1,11	0.19	0.670
Chain (CH)	1.3,14.3	20.03	0.000*
Site (ST)	1.4,15.5	52.80	0.000*
CC*CH	1.4,15.4	1.00	0.362
CC*ST	1.4,15.9	1.76	0.207
CH*ST	2.2,24.5	1.09	0.358
CC*CH*ST	1.7,18.7	1.62	0.227

* indicates statistical significance at the 0.05 level or better

Target v rare non-target

The P300 elicited by the target novel sound had a mean latency of 310 ms and that elicited by the rare non-target tone had a mean latency of 313 ms, the difference in latency was not significant (t=-0.32, P=0.75).

The results of the ANOVA on the amplitude of the P300 elicited by the two categories of rare stimuli are shown in Table 8.3. It can be seen that the P300 elicited by the target novel sound was significantly larger in amplitude than that elicited by the rare non-target tone.

A significant main effect of chain was found which interacted significantly with condition. Newman Keuls comparison of amplitude across chain, for each condition, showed that for the targets amplitude was larger at midline than at lateral sites and larger at right than left hemisphere sites, whereas for the rare nontargets amplitude was larger at midline than lateral sites but no differences were seen between lateral sites.

A significant main effect of site was obtained on the amplitude of the P300 elicited by the two categories of rare stimuli. Table 8.3 shows that site interacted significantly with condition. Newman Keuls tests were used to investigate the interaction. The P300 elicited by the target novel sound was significantly larger in amplitude at parietal than at central and frontal sites and was significantly larger at central than frontal sites. In contrast, that elicited by the rare non-target tone did not differ in amplitude between central and parietal sites but was significantly larger at both than at frontal sites.

Target v rare non-target after rescaling

The results of the ANOVA on the rescaled data, given in Table 8.3, show a significant main effect of chain. Newman Keuls comparison of rescaled amplitude across chain, collapsed over condition and site, showed the P300 to have a significant midline maximal distribution (see Figure 8.2).

A significant main effect of site was obtained. The P300 was found to be maximally distributed over parietal sites. Newman Keuls comparison of amplitude across site, collapsed over condition and chain, showed that the P300, elicited by both categories of rare stimuli, was distributed significantly more over parietal sites than over central and frontal sites and significantly more over central than frontal sites (see Figure 8.3).

The absence of significant interactions between condition and chain, and condition and site (see Table 8.3) indicate that the scalp distribution of P300s elicited by the two categories of rare stimuli did not differ.

N100 before rescaling

The N100 peak was found to have a mean latency at Cz of 103 ms in the waveforms elicited by the frequent novel sound, 98 ms in those elicited by the target novel sound and 98.3 ms in those elicited by the rare non-target tone. No significant difference was found between the latency of the N100 elicited by stimuli in the three conditions ($F(1.6,17.8)=1.907$, $P>0.05$).

Figure 8.2 Graph illustrating distribution, across chain, of rescaled amplitude of the P300 deflection elicited by targets and rare nontargets in experiment 5.

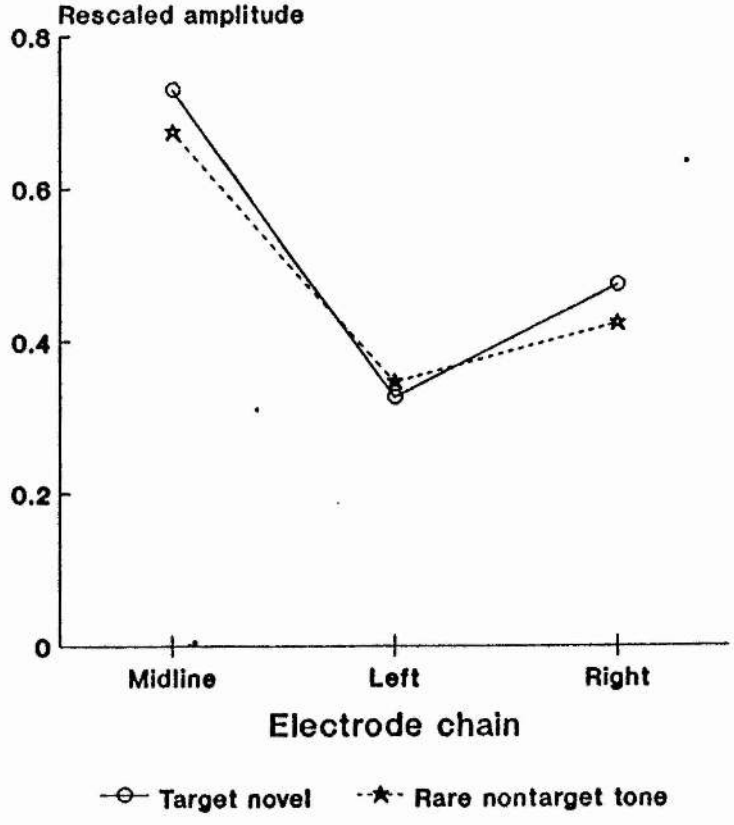
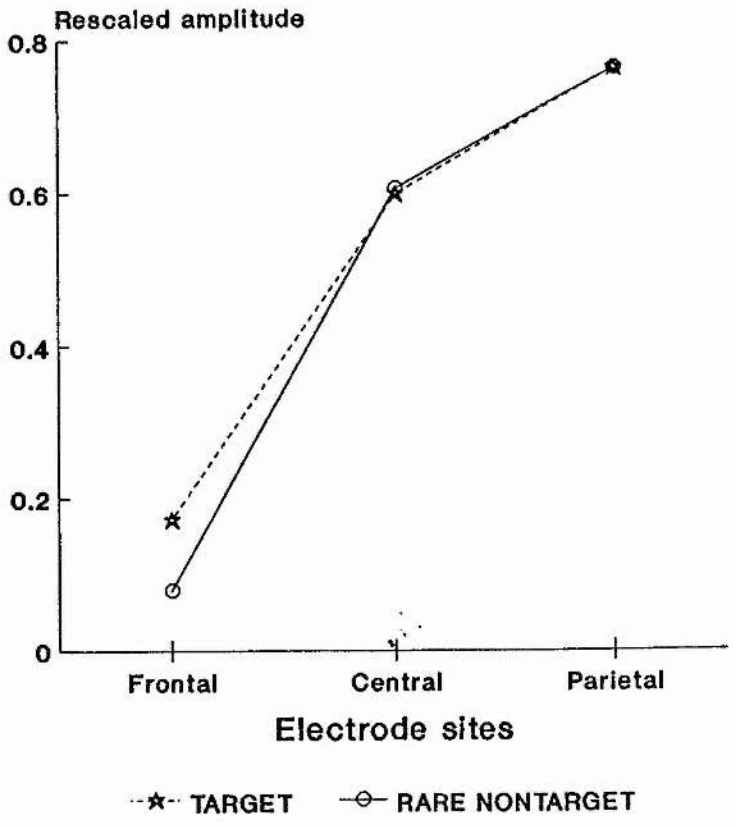


Figure 8.3 Graph illustrating distribution, across site, of rescaled amplitude of the P300 deflection elicited by targets and rare nontargets in experiment 5.



As shown in the results of the ANOVA displayed in Table 8.4 of the Appendix, the amplitude of the N100 differed significantly between conditions. A Newman Keuls test comparing the amplitude of the N100 across condition, collapsed over site and chain, showed that the N100 elicited by the rare non-target tone was significantly larger in amplitude than that elicited by the target and frequent novel sounds. The N100 elicited by the frequent novel sound was significantly larger than that elicited by the target novel sound. A significant condition by site interaction was obtained because the difference in amplitude between the N100 elicited by the rare tone and that elicited by the rare and frequent novel sounds was significantly larger at frontal sites than at central and parietal sites (Newman Keuls tests comparing the difference in N100 amplitude between conditions, across site).

The interactions between condition and site, and chain and site, are important for understanding the scalp distribution of the N100 and will therefore be discussed further in relation to the analysis of the rescaled data.

N100 after rescaling

As shown in Table 8.4 of the Appendix, significant main effects of chain and site were obtained in the analysis of the rescaled N100 amplitude data.

A significant condition by site interaction was obtained (see Figure 8.4). The interaction was investigated by performing Newman Keuls post hoc comparisons of N100 rescaled amplitude across site, collapsed over chain, for each condition. It was found that the N100 elicited by both the frequent and target novel sounds was significantly more negative at central than parietal sites but showed no significant differences between frontal and central, and frontal and parietal sites. In contrast,

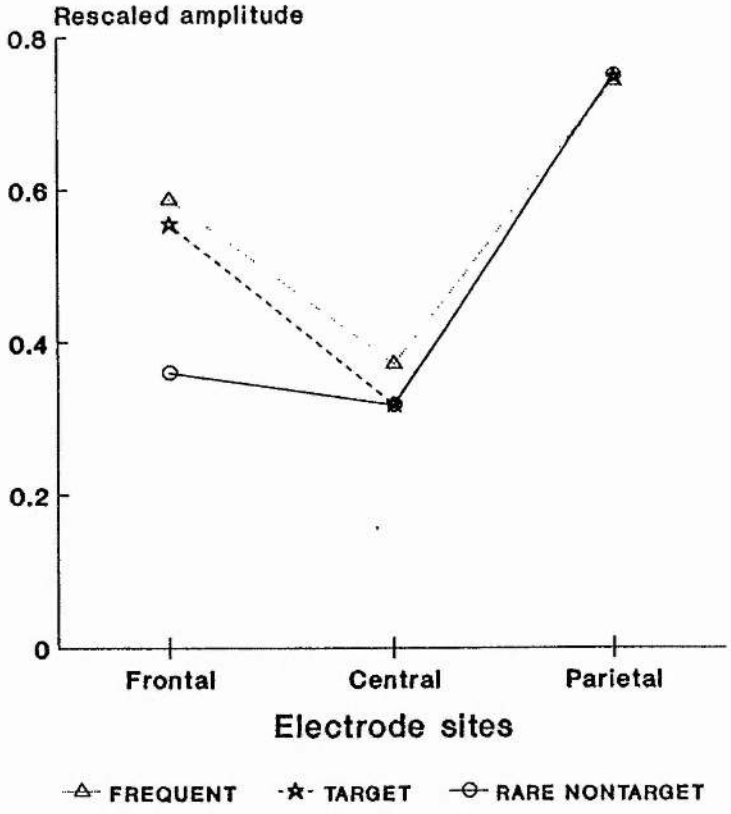


Figure 8.4 Graph illustrating distribution, across site, of rescaled amplitude of the N100 deflection elicited by targets and rare nontargets in experiment 5.

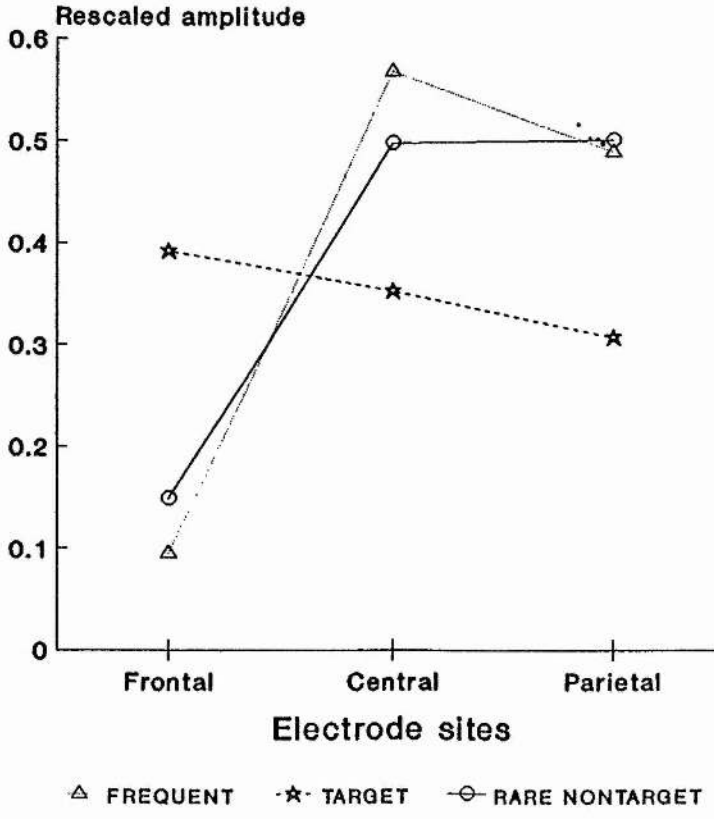


Figure 8.5 Graph illustrating distribution, across site, of rescaled amplitude of the P170 deflection elicited by targets and rare nontargets in experiment 5.

the N100 elicited by the rare non-target tone was significantly more negative at frontal and central sites than at parietal sites but did not differ between central and frontal sites.

Table 8.4 of the Appendix shows a significant chain by site interaction. It was found that at the midline the N100 was significantly larger at central than parietal sites but did not differ significantly between frontal and central or frontal and parietal sites. Over the left hemisphere no significant differences in N100 rescaled amplitude were found between sites. Over the right hemisphere, the N100 was found not to differ significantly between frontal and central sites but was significantly more negative at both than at parietal sites.

P170 before rescaling

The P170 peak was found to have a mean latency of 186.4 ms in the waveforms elicited by the frequent novel sound, 165.6 ms in those elicited by the target novel sound and 176.4 ms in those elicited by the rare non-target tone. A significant difference in P170 latency was found between the three conditions. The latency of the P170 elicited by the frequent stimuli was significantly longer than that elicited by both the target and rare non-target stimuli and the P170 elicited by the rare non-target stimuli had a significantly longer latency than that elicited by the targets (Newman Keuls comparison of P170 latency (measured at Fz) across condition).

As shown in the results of the ANOVA given in Table 8.5 of the Appendix, significant main effects of condition, chain and site were found on P170 region amplitude. A significant condition by chain interaction was obtained. A Newman Keuls comparison of P170 region amplitude across condition for each chain showed

that at the midline the P170 elicited by the targets and frequents did not differ but both were significantly larger in amplitude than that elicited by the rare nontargets. Over lateral sites no significant differences in P170 region amplitude were found between conditions.

Table 8.5 of the Appendix shows a significant interaction between condition and site. Newman Keuls tests comparing the amplitude of the P170 across condition for each site showed that the interaction was obtained because at frontal sites the P170 elicited by the rare target novel sounds was significantly larger than that elicited by the frequent novel sounds and the rare non-target tone. A significant chain by site interaction was found which will be discussed in relation to the analysis of the rescaled data.

As the P170 deflection is superimposed on the rising slope of the P300 deflection, it is possible that differences in amplitude of the P170 between conditions may actually be due to amplitude differences between the P300 deflection elicited by stimuli in the three conditions. The P300 deflection, however, is distributed maximally over central and parietal sites and so will have a minimum influence on P170 amplitude at frontal sites. The ANOVA was therefore performed again on the data but selecting only the frontal three electrode sites. A significant main effect of condition was obtained ($F(1.6,17.6)=10.028$, $P<0.005$) which interacted significantly with chain ($F(2.4,26.5)=3.735$, $P<0.05$). The interaction was produced because the P170 elicited by the frequent and target novel sounds at frontal sites was distributed maximally over the midline whereas that elicited by the rare non-target tone did not differ in amplitude between the electrode chains. Newman Keuls tests comparing the difference between chains across conditions showed that the difference between midline and left and midline and right hemisphere sites was significantly larger for

the P170 elicited by the target novel sounds than for the frequent and rare non-target stimuli and was significantly larger for the P170 elicited by the frequent novel sound than for the rare non-target tone. In contrast, the difference in amplitude between left and right hemisphere sites did not differ significantly between conditions.

P170 after rescaling

The results of the analysis of the rescaled amplitude data (see Table 8.5 of Appendix) show a significant main effect of chain which did not interact significantly with condition. Newman Keuls comparison of rescaled amplitude across chain, collapsed over condition and site, showed the P170 region to be distributed maximally over midline electrodes.

A significant main effect of site was obtained which interacted significantly with condition. The scalp distribution for each condition at midline sites is shown in Figure 8.5. The figure shows that the P170 region in the waveforms elicited by frequent and rare non-target stimuli was larger over central and parietal sites than over frontal sites. In contrast, the P170 deflection elicited by the target did not differ in amplitude across site. Newman Keuls tests showed that the difference between the rescaled amplitude of the P170 region elicited by the frequent novel sound and that elicited by the rare non-target tone did not differ significantly across site. In contrast, the comparison of the difference in the rescaled P170 amplitude between the frequent novel sound and the target novel sound and between the rare non-target tone and the target novel sound showed that in both cases, the difference did not differ significantly between parietal and central sites but differed significantly between both these sites and that at frontal sites. This was because at frontal sites the P170 region elicited by the targets was more positive than that elicited by the

frequent and rare non-target stimuli whereas at central and parietal sites the same region was less positive than that elicited by the frequents and rare non-targets.

Table 8.5 of the Appendix shows a significant interaction between chain and site. The interaction was obtained because the P170 region was found to be maximally distributed over central and parietal sites at the midline but showed no significant differences between electrodes at lateral sites (Newman Keuls comparison of amplitude across site for each chain).

500-900 ms region before rescaling

As can be seen from the results of the ANOVA given in Table 8.6 of the Appendix, no significant main effect of condition was found on the amplitude of the 500-900 ms region of waveform.

A significant main effect of chain was found which interacted significantly with condition. Newman Keuls comparison of the amplitude of the 500-900 ms region across chain for each condition showed that for the frequent and rare non-target stimuli this region of the waveform showed no significant difference between chains, whereas the 500-900 ms region in the waveforms elicited by the targets showed significantly larger amplitude at right hemisphere and midline sites than at left hemisphere sites but no significant difference in amplitude between right hemisphere and midline sites.

Table 8.6 of the Appendix shows a significant main effect of site which interacted significantly with condition. Newman Keuls comparison of the amplitude of the 500-900 ms region across site for each condition showed that this region in the

waveforms elicited by the frequent stimuli showed no significant difference in amplitude between sites. The 500-900 ms region elicited by the target novel sound was significantly larger at parietal sites than at central and frontal sites and significantly larger at central than at frontal sites. The 500-900 ms region elicited by the rare non-target tone did not differ significantly in amplitude between central and parietal sites but was significantly larger at both than at frontal sites. A Newman Keuls comparison of the difference in the amplitude of the 500-900 ms region elicited by the targets and rare non-targets at each site (collapsed over chain) showed that there was a significantly greater difference in amplitude between conditions at parietal than at central and frontal sites and at central than frontal sites. This was because at frontal sites there was no difference in amplitude between the 500-900 ms region elicited by the two categories of rare stimuli, whereas at parietal sites this region of the waveform was more positive in response to the targets than in response to the rare non-targets. The chain by site interaction will be discussed in relation to the analysis of the rescaled data.

500-900 ms region after rescaling

As shown in Table 8.6 of the Appendix, the amplitude of the 500-900 ms region did not differ significantly between electrode chains and the interaction between condition and chain was not present in the analysis of the rescaled data.

Table 8.6 of the Appendix shows a significant main effect of site which did not interact significantly with condition. Newman Keuls comparison of rescaled amplitude across site collapsed over condition and chain showed that the 500-900 ms region of the waveform was larger at parietal and central sites than at frontal sites but did not differ significantly between parietal and central sites.

Table 8.7. Mean reaction time (ms) to respond to target novel sound, mean number of hits, mean number of false alarms and corresponding standard deviations (SD) in auditory oddball task of experiment 5.

	MEAN	SD
Reaction time	397.0	99.6
Number of hits	44.7	0.9
Number of false alarms	0.8	1.1

Table 8.6 of the Appendix shows a significant chain by site interaction. The interaction was obtained because the 500-900 ms region was distributed maximally over parietal sites at the midline whereas at lateral sites it showed a central maximal distribution.

Behavioural Data

A summary of the behavioural data is given in Table 8.7. The time required to respond to the target novel sound in the present experiment was significantly shorter than that required to respond to the target tone in Experiment 1 ($t=2.35$, $P=0.028$). No significant difference was found, between the two experiments, in the number of hits ($t=-0.93$, $P=0.36$) and number of false alarms ($t=-1.24$, $P=0.23$).

Between Experiment comparisons

ANOVA comparing P300 elicited by rare nontargets in experiment 1 with that elicited by rare nontargets in experiment 5 showed P300 to be significantly larger in amplitude in experiment 1 than in experiment 5 ($F(1,22)=32.086$, $P<0.001$). A significant experiment by chain interaction was obtained ($F(1.6,34.7)=14.995$, $P<0.001$), Newman Keuls comparison of P300 amplitude across chain, for each experiment, showed that for both experiments the P300 was significantly larger at midline than lateral sites which did not differ but inspection of the means showed the interaction to be due to this difference being larger in experiment 1 than in experiment 5. No significant differences were found between experiment and site ($F(1.5,33.0)=1.357$, $P>0.05$) or experiment, chain and site ($F(2.8,60.9)=1.601$, $P>0.05$).

ANOVA comparing P300 elicited by target tones in experiment 1 and target novel sounds in experiment 5 showed amplitude of the P300 to be significantly larger in experiment 5 ($F(1,22)=13.734$, $P=0.001$). A significant experiment by chain interaction was obtained ($F(1.6,35.2)=11.899$, $P<0.001$) because in experiment 1 the target P300 showed no significant difference in amplitude between chains, whereas in experiment 5 the target P300 amplitude was significantly larger at midline than lateral sites and significantly larger at right than left hemisphere sites (Newman Keuls comparison of P300 across chain for each experiment). No significant interactions were found between experiment and site ($F(1.3,28.6)=3.037$, $P>0.05$) or experiment, chain and site ($F(2.7,60.1)=0.5$, $P>0.05$).

ANOVA comparing P300 elicited by target tones in experiment 1 and rare nontarget tones in experiment 5 showed no significant difference between experiments ($F(1,22)=0.024$, $P>0.05$) and no significant interactions between experiment and chain ($F(1.6,36.1)=1.706$, $P>0.05$) or experiment, chain and site ($F(3.1,68.4)=2.093$, $P>0.05$). A significant experiment by site interaction was obtained ($F(1.4,30.4)=5.158$, $P<0.05$) because in experiment 1 the P300 deflection was significantly larger at parietal than at central and frontal sites and significantly larger at central than frontal sites, whereas in the present experiment the P300 deflection was significantly larger at parietal and central sites than at frontal sites but no significant difference was found between parietal and central sites (Newman Keuls comparison of P300 across site for each experiment).

ANOVA comparing the rescaled amplitude of the P300 deflection elicited by targets in experiment 1 with that elicited by targets in experiment 5 showed no significant main effect of experiment ($F(1,22)=0.772$, $P>0.05$) and no significant interaction

between experiment, chain and site ($F(2.9,63.2)=1.035$, $P>0.05$). A significant experiment by chain effect was obtained ($F(1.8,39.7)=5.401$, $P<0.05$) because in experiment 1 no significant difference in P300 was found across chains, whereas in experiment 6 the P300 deflection was significantly larger at midline than lateral sites which did not differ (Newman Keuls comparison of P300 across chain for each experiment). A significant interaction was also obtained between experiment and site ($F(1.3,28.8)=4.466$, $P<0.05$). The interaction was produced because the P300 elicited by the target novel sounds in the present experiment was distributed more over central sites than that elicited by the target tones in experiment 1. A centro-parietal maximum, in contrast to a parietal maximum, was obtained.

ANOVA comparing P300 elicited by targets in experiment 1 with that elicited by rare nontargets in experiment 5 showed no significant main effect of experiment ($F(1,22)=0.178$, $P>0.05$) and no significant interactions between experiment and chain ($F(1.6,35.4)=2.115$, $P>0.05$) or experiment, chain and site ($F(3.1,68.2)=2.032$, $P>0.05$). A significant experiment by site interaction was obtained ($F(1.4,30.7)=4.424$, $P<0.05$) because in experiment 1 P300 was significantly larger at parietal than central and frontal sites and significantly larger at central than frontal sites, whereas in experiment 5 P300 did not differ significantly between central and parietal sites but was significantly larger at both sites than at frontal sites (Newman Keuls comparison of P300 across site for each condition).

Summary of results

A P300 deflection with a parietal maximal distribution was elicited in response to both the rare target novel sounds and rare nontarget tones. The P300 elicited by both categories of rare stimuli had a midline maximum distribution. The amplitude

of the P300 deflections were significantly larger than the same region of waveform elicited by the frequent novel sounds. The latency of the P300 elicited by the two categories of rare stimuli did not differ significantly. Results of the ANOVAs comparing the P300 deflections elicited in the present experiment with those elicited in experiment 1 showed that, although the P300 elicited by both the target novel sounds and nontarget tones had a parietal maximum, they were more anteriorly distributed than the P3b elicited by target tones in experiment 1. The N100 was found to be significantly larger in amplitude in response to the nontarget tones than in response to both categories of novel sounds. This amplitude difference was more pronounced at frontal than central and parietal sites. The N100 elicited by the tones had a more anterior distribution than that elicited by the two categories of novel sounds. At frontal sites, the P170 elicited by the rare target novel sounds was significantly larger in amplitude than that elicited by the other two categories of stimuli. The P170 elicited by the target novel sounds was distributed more over frontal sites and less over central and parietal sites than that elicited by the other two categories of stimuli. The 500-900 ms region of waveforms elicited by the frequents did not differ significantly between sites, whereas for both categories of rare stimuli the 500-900 ms region was more positive at parietal sites than at frontal sites. At frontal sites, the 500-900 ms region elicited by the two categories of rare stimuli did not differ significantly in amplitude, at parietal sites however, the 500-900 ms region elicited by the target novel sounds was more positive than that elicited by the rare tones.

DISCUSSION

A positive deflection was elicited with a mean latency of 310 ms in response to the targets and 313 ms in response to the rare non-targets. This deflection was considered to be produced by a component, or overlapping components, of the P300 complex. Only a very small positive deflection with a similar latency was elicited in response to the frequent stimuli.

Although the analysis of the raw amplitude data suggested that the P300 elicited by the rare non-target tone was more anteriorly distributed than that elicited by the target novel sound, this difference in distribution of the P300 across site was not present in the analysis of the rescaled P300 amplitude data. The analysis of the rescaled data showed the P300 elicited by both the target and rare non-target to be maximally distributed over parietal sites. The scalp distribution of the P300 deflection, elicited by both categories of rare stimuli, suggests a greater contribution to the waveform of the P3b component than the more anterior P3a component. The results are therefore inconsistent with the hypothesis proposed in the Introduction, that detection of a mismatch between the presented stimulus and a sensory trace of the features of the frequent stimulus, is sufficient to elicit a P3a.

The between experiment analyses suggested that the P300 elicited by the rare nontarget tones and target novel sounds in the present experiment were more anteriorly distributed than the P300 elicited by the target tones of experiment 1. This difference in scalp distribution may indicate a contribution of anterior activity to the deflection in the present experiment which was not present in the deflection elicited by the targets in experiment 1. Despite this difference in distribution

between experiments, the P300 still had a parietal maximum in the present experiment indicating a P3b rather than a P3a distribution.

The analysis of the rescaled P300 data showed that the P300 deflection elicited by both categories of rare stimuli was distributed maximally over midline electrodes. This contrasts with the distribution of the P3b elicited by target tones in Experiment 1 which showed no difference in amplitude across electrode chains. This suggests that the activity of a generator additional to that activated in Experiment 1 may be contributing to the P300 deflection elicited by the targets in the present experiment.

The P300 deflection elicited by the target novel sound was significantly larger in amplitude than that elicited by the rare non-target tone. This contrasts with Experiment 1 where the rare non-target novel sound elicited a P300 of larger amplitude than the target tone. This result of Experiment 1 suggests that in the present experiment, the target novel sound did not produce a P300 deflection of larger amplitude than the rare non-target tone because it was a target. It could be suggested that a P300 of larger amplitude was produced in response to the target novel sound because of overlap of a P3a and P3b component in the present experiment which was not present in Experiment 1. It is suggested that the P3a would have been produced because of detection of a mismatch between the target and the trace of the frequent stimulus held in sensory memory and the P3b would have been produced because of further processing of the stimulus following stimulus identification. However, the scalp distribution of the P300 elicited by the target is posterior suggesting that it is unlikely that the amplitude is being increased simply by the addition of more anteriorly distributed activity. It is possible that the target elicited both a greater amount of posterior activity and anterior activity in the present experiment compared with the rare nontarget in the present experiment and

the target in experiment 1. The amplitude of the P300 deflection would therefore have increased but the posterior distribution would have been maintained. Alternatively, the target novel sound may have elicited a P300 of larger amplitude than the rare nontarget tone of the present experiment and the target tone of experiment 1 because of the complexity of the novel sound stimulus compared with a simple tone. Data reviewed by Johnson (1988) suggest that P300 amplitude is directly related to stimulus complexity.

Only a small positive deflection was present, in the waveforms elicited by the frequent stimuli, within the latency window in which the P300 deflection was elicited by the two categories of rare stimuli. This finding is consistent with previous reports of the effects of subjective probability on the P3b. The amplitude of the P3b has been found to be larger for stimuli which have a smaller temporal probability (temporal probability being the probability of the occurrence of a stimulus within a certain period of time). As the temporal probability of the frequent novel sound is high in the present experiment, only a small P3b (if any) would be expected. The finding that a P3a was not elicited by the frequent novel sound suggests that novel sounds do not automatically elicit a P3a irrespective of their probability of occurrence or the other stimuli in the task. This finding is therefore consistent with conclusions drawn from the previous experiments that a P3a is elicited by a novel sound only if it occurs rarely and does not match features of a frequently occurring stimulus held in a sensory memory trace. As discussed previously, it is possible that the frequent stimuli elicited a P3a when initially presented or immediately following presentation of a different stimulus. On repeated presentation of the frequent stimulus, however, a trace of the frequent would have been formed in sensory memory so that on subsequent presentations of

the stimulus a match would be detected. Due to the absence of a mismatch, no orienting of attention would occur to the stimulus and no P3a would be elicited.

The N100 elicited by the rare non-target tone was significantly larger in amplitude than that elicited by both the target and frequent novel sound. Due to the high temporal probability of the frequent novel sound, the neurons activated by its presentation, whose activity contributes to the N100 deflection, would have been in a refractory state on the next presentation of the frequent novel sound. Only a small N100 would therefore be elicited by the frequent novel sound. It is possible that there was an overlap in the neurons contributing to the N100 deflection which were activated by the frequent and target novel sound. This is possible because the N100 is thought to be produced in response to physical characteristics of the stimulus such as a change from one level of physical energy to another and so are sensitive to transient aspects of stimuli (Graham, 1979; Loveless, 1983; MacMillan, 1973) and the two novel sounds share a number of features such as fast onset time and duration which are not shared with the rare non-target tone. The neurons activated by both the frequent and target novel sound would therefore be in a refractory state when the next target sound is presented causing a smaller N100 to be elicited than when the two categories of stimuli do not activate overlapping groups of neurons. The N100 produced would not, however, be as small in amplitude as that produced by the frequent novel sound. This is because the target novel sound would additionally activate neurons not activated by the frequent novel sound which, due to the long temporal interval between target tones. would not be refractory on the next presentation of a target stimulus. As the rare non-target tone shares few features with the two novel sounds, the neurons activated by the tone, whose activity contribute to the N100 deflection, would be expected to differ from those activated by the novel stimuli. The temporal interval between the rare non-target tones was

large, so the neurons would have recovered from a refractory state by the next presentation of a tone. The N100 elicited by the tone would therefore be expected to be larger than that elicited by the novel sounds which is consistent with results reported here.

As discussed in Experiment 1, the difference in distribution of the N100 between conditions may be due to differences in the combination, or strength, in different conditions, of a number of generators whose activity contributes to the N100 deflection. The results from the present experiment and experiment 1, suggest that tones elicit an N100 with a fronto-central maximum, whereas, novel sounds elicit an N100 which is less anteriorly distributed. These distributions occur irrespective of the probability or role of the stimulus in the task. This therefore confirms the suggestion that the N100 is dependent on physical features of the stimuli as well as more psychological factors such as direction of attention.

As discussed in Experiment 1, the P170 peak probably reflects overlapping contributions to the waveform of activity of a P165 and P200 generator. The P200 is thought to be produced in response to all attended stimuli, whereas the P165 is only produced in response to rare attended stimuli (Goodin et al., 1978). In the present experiment, the latency of the P170 was found to differ significantly between conditions. This latency difference probably reflects the differing strength of activation of the P165 and P200 generators in response to stimuli of each condition. The longer latency of the P170 deflection elicited by the frequent stimuli in the present experiment suggests that it may be reflecting a contribution to the waveform of a P200 component. In contrast, the earlier latencies of the P170s elicited by the two categories of rare stimuli probably reflect overlapping contributions to the waveforms of P165 and P200 components.

It has been suggested that the presence of the P165 in the ERP waveforms elicited by attended rare stimuli is due to the increased processing of the rare stimulus when attended and may reflect processes involved in stimulus identification and classification or response selection (Goodin et al., 1978). In the present experiment, the P170 elicited by the rare novel stimulus was significantly larger in amplitude than that elicited by the rare tone. It is possible that this is because the novel sound requires more processing than the tone because it is a target or because it is more difficult to identify or categorise than the tone. In Experiment 1, the P170 elicited by the novel sound (rare non-target) was larger in amplitude than that elicited by the target, although this difference was small. It is therefore suggested that the larger P170 elicited in response to the target novel sound in the present experiment is produced because of characteristics of the stimulus such as the extent to which it captures attention and how difficult it is to categorise rather than its role of target in the task. It may be that the difference in amplitude of the P170 between novel sounds and tones is not due to a difference in the strength of activation of the 'P170 generator' but due to a difference in the amplitude of the N100 deflection elicited by tones and novel sounds which may overlap the P170. The scalp distribution of the P170 region was similar to that of the P300 showing greater positivity over central and parietal sites than over frontal sites. This was because the P170 was superimposed on the rising slope of the P300. It is therefore possible that differences in the pre-stimulus baseline to peak amplitude of the P170 between conditions are due to differences in the amplitude of the P300 or to differences in the size of the N200 deflection which is superimposed on the rising slope of the P300, following, but possibly overlapping, the P170.

Inspection of the 500-900 ms region of the waveform showed that a negative slow wave was produced at frontal sites and a positive slow wave produced at parietal sites in response to all stimuli. The negative frontal slow waves elicited by the target novel sound and the rare non-target tone were found not to differ significantly in amplitude. In contrast, the positive slow wave at parietal sites was larger in response to the target novel sound than in response to the rare non-target tone. A dissociation between the frontal negative and posterior positive slow waves was therefore obtained in the present experiment. If the negative and positive slow waves were reflecting the activity recorded from opposite ends of a generator which could be modelled by an equivalent dipole, any difference in amplitude between the two conditions would be the same at both frontal and parietal sites, that is if there was no difference in amplitude between the two conditions at frontal sites there would be no difference between conditions at parietal sites (equivalent dipoles are discussed by Scherg, 1989). This was not the case in the present experiment. The results of the analysis of the amplitude of the 500-900 ms region provide further support for a dissociation between the frontal negative and posterior positive slow waves and suggest that the frontal negative slow wave is reflecting further processing of both categories of rare stimuli, whereas the process generating the posterior positive slow wave appears to be activated more by the targets than rare non-targets.

The number of hits and false alarms made by subjects suggested that, as in Experiment 1, performance on the task was at ceiling. The time taken to respond to the targets was significantly shorter in the present experiment than in Experiment 1 indicating that the subjects found the present task easier than that in which the target was a tone. As discussed in relation to the results of Experiment 2, it is possible that when the frequent and target stimuli are tones, and therefore vary along a continuum

of frequency, they are more difficult to discriminate than frequent and target stimuli which are distinct novel sounds. Faster reaction time would be predicted in the latter case which was as obtained in the present experiment.

Summary

The main finding of the present experiment was that a P300 deflection with a parietal maximum was elicited by rare non-target tones when the frequent stimulus was a novel sound. This contrasts with the results of Experiments 1 and 6 in which rare non-target novel sounds elicited a P300 deflection with a centro-parietal maximum when the frequent stimulus was a tone. The more anteriorly distributed P300 deflection elicited in experiments 1 and 6 is thought to reflect the contribution to the waveform of the P3a component. The results of the present experiment were not consistent with the predictions of Naatanen (1990). According to Naatanen a neuronal trace of the physical features of the frequent stimulus should have been formed in sensory memory. On presentation of the rare non-target tone, a comparison would have occurred between the features of the rare non-target and those represented in the neuronal trace. The physical difference between the frequent and rare non-target stimuli was the same in the present experiment as in Experiments 1 and 6, the only difference between experiments being that the conditions to which the stimuli were assigned were reversed. In Experiments 1 and 6 the rare non-target novel sound elicited a P3a. As the P3a is thought to result from detection of a mismatch, it was predicted that a P3a would also be elicited by the rare non-target stimuli in the present experiment. This ERP component appeared not to be making a major contribution to the P300 deflection in the present experiment. This suggests that although detection of a mismatch may be necessary for the elicitation of the P3a, it is not sufficient. The finding that a P3b was elicited

by the rare non-target stimuli suggested that the stimuli gained access to conscious processing but it is suggested that this may not be via the mismatch detection route.

CHAPTER 9

EXPERIMENT 6: INVESTIGATION OF THE HABITUATION AND DISHABITUATION OF P3A DURING ONE EXPERIMENTAL SESSION

INTRODUCTION

According to Naatanen (1990), the P3a component of the P300 complex is thought to reflect processes related to the orienting of attention.

The orienting reflex (OR) was first described by Pavlov (1928), who noticed that during conditioning experiments reflexive attentional reactions occurred in response to occasional environmental distractions. Pavlov described the behavioural response resulting from this as the 'what's that?' or orienting reflex.

Most contemporary investigations and ideas concerning the OR have developed from the work of Sokolov (1960,1963,1969,1975). The orienting response to occasional, unexpected or significant stimuli has been dissociated from adaptation, defense and startle responses. The adaptation response is dependent on the quality of stimulation, for example opposite responses would occur to warmth and cold. Warmth would dilate cerebral and peripheral blood vessels, whereas cold would constrict them. The defense response is dependent on stimulus intensity and occurs to sustained presentation of a stimulus of increased intensity. The defense response is thought to be involved in facilitation of output or motor-response preparation (Graham, 1979). In contrast, the startle response is a reflex which occurs without cortical involvement and is triggered by transient change (Graham, 1979). Sokolov

(1975) defined the OR as having a low threshold for its release compared with the thresholds for adaptive and defensive responses, causing generalised excitation of the organism with the absence of a specific reflex response and showing extinction on repeated presentation of the stimulus (habituation). Changing a parameter of the stimulus, for example if the stimulus is "intensified, weakened, lengthened, shortened; when it is presented before the usual time, when it is omitted at the usual time (Sokolov, 1969)" caused an OR to be released and caused subsequent presentation of the original stimulus to elicit an OR. The release of the OR by the original stimulus after its habituation, following presentation of a changed stimulus, has been called dishabituation. However, the habituated stimulus and the same stimulus presented after stimulus change have been found to elicit similar responses in a number of psychophysiology studies. Due to these similar responses many researchers have focused on recovery of the OR to stimulus change and referred to this as dishabituation (Loveless, 1983). Habituation and dishabituation are the defining characteristics used by most authors to distinguish the OR from adaptation and defense responses eg. Kahneman (1973), Siddle and Spinks (1979).

Sokolov thought that the OR reflected the detection of novelty, probably through a matching process of the presented stimulus against internal representations (neuronal models) of previously presented stimuli. These representations were thought to incorporate features such as stimulus quality, rate of presentation, associated behavioural responses and contextual information. Failure of a match causes the OR which is reflected by autonomic and behavioural changes which allow the organism to respond readily to the stimulus. On repeated presentation, a neuronal model of the stimulus is established and the size of the OR decreases. Stimulus significance, however, retards the habituation of the OR (Sokolov, 1960, 1963). Sokolov refers mainly to the OR elicited by novel but harmless stimuli which do not require a

response, he considers the OR elicited by significant stimuli to represent a special subclass of OR. Bernstein and Taylor (1979) have a different view, he argues that an OR does not occur to every change in stimulation but only to that which is significant. He argues that when stimuli are initially presented they are all considered to be significant, whether they require a response or not, but that rapid habituation occurs as the subject realises that a particular stimulus has no special relevance. The signal stimuli, which would require a response on every presentation, would continue to elicit an OR throughout the task.

In contrast to Sokolov, Siddle and Spinks (1979) suggest that the "functional significance of the OR can be viewed with reference to facilitation of perception of future stimuli rather than facilitation of perception of the eliciting stimulus". The authors have presented evidence in support of this showing that electrodermal responses following a warning stimulus are larger when the stimulus signals high information than when it signals low information.

It has been suggested (eg. Kahneman, 1973; Sokolov, 1969) that the OR is not a single response but a number of responses which can be dissociated. The components of the OR include an increased skin conductance, inhibition of ongoing activity, gross realignment of the head and receptor orientation and postural adjustments, pupil dilation, heart rate deceleratory and possibly acceleratory phases, respiratory pause/lability, peripheral vasoconstriction and cephalic vasodilation, nonspecific electromyographic (EMG) activity, desynchronisation of EEG rhythms and patterned changes in spinal and blink reflexes.

In addition to the OR components listed above, a number of ERP components have been related to the OR. The N1 and immediately following P2 show habituation

which closely parallels the course of electrodermal and heart rate OR habituation (Rust, 1977; reviews by Callaway, 1973; Ohman and Lader, 1977). It has been suggested by Naatanen and Gaillard (1983) that the N1-P2 complex may be related to the initial OR which occurs to isolated stimuli and the initial stimulus of a sequence. A relation between N1-P2 and the OR has been suggested because its habituation shows the general characteristics of recovery to change, generalisation of habituation, effects of rate and spontaneous recovery. Ohman and Lader (1977), however, conclude that N1 is not an OR component because, unlike the OR, its habituation is insensitive to attentional factors. The MMN follows the N1-P2 complex and has been suggested by Naatanen and Gaillard (1983) to represent a "preperceptual" and "automatic cerebral process which is a necessary, but not a sufficient condition for the conscious perception of stimulus deviance". Woldorff et al. (1991) have presented evidence questioning the independence of the MMN from direction of attention. This was discussed more fully in Chapter 1. It was suggested by Naatanen and Gaillard that the process reflected by the MMN was identical to the match-mismatch process hypothesised by Sokolov, particularly the version in which the physical features of the stimuli are emphasised (Sokolov, 1975). Occurrence of the MMN was not thought to be sufficient for OR elicitation. Naatanen and Gaillard (1983) suggest that the full scale OR only occurs when the N2b-P3a complex is elicited. As discussed in Chapter 1, the P3a is thought to reflect a process which is the precursor of an attentional switch resulting from detection of a mismatch between the presented stimulus and a neuronal trace of the physical features of the frequently occurring preceding stimuli. The attentional switch allows the presented stimulus to gain access to processing whose results are available to consciousness.

The P3b component of the P300 complex also has a large literature linking it with the OR (reviewed by Friedman, 1978; Donchin, 1981; Roth, 1983). There is,

however, a major problem in the interpretation of this literature due to the difficulty in separating P3a and P3b components. This means that effects attributed to the P3b may actually result from changes in the P3a. The reported similarities between the P3b and the OR include eliciting conditions, for example novelty, signal value, relevance, intensity, rate and variability of stimulation and deviation from expected stimulation (Roth, 1983). The amplitude of the P3b has also been found to be related to the size of simultaneous autonomic measures, an example of which would be pupil dilation (Friedman et al., 1973). A number of poor associations with autonomic measures have also been reported. Donchin (1981) has related the P3b to processes involved in updating the neuronal model and experimental expectancies. This process has also been emphasised by Sokolov (1969) who suggests that "the neuronal model of a stimulus can not be thought of as some static imprint. Rather, it constantly undergoes revisions in order to account for the stimulus which is operating at a given moment". Slow waves following the P3b have also been related to the OR.

It is probable that no one ERP component can be identified with the OR because the OR appears to involve a number of output functions such as suppression of ongoing activity and facilitation of sensory input. These processes would involve different anatomical structures and, therefore, would be expected to be reflected by different ERP components. Initial and change ORs were distinguished because of the occurrence of different ERP components in the two situations. The presentation of isolated stimuli causes the elicitation of the N1-P2 complex which is responsive to stimulus onsets and offsets. This complex is thought to be related to the initial OR. Change of stimulation within a sequence causes the additional elicitation of the N2b-P3a complex which is dependent on prior occurrence of the MMN. This complex is thought to be related to the change OR (Loveless, 1983). The habituation of the N1-

P2 complex is affected by changes in the rate of stimulus presentation, whereas the N2b-P3a complex is unaffected; this suggests that the initial and change ORs are separable (Loveless, 1983).

It has been suggested that a defining characteristic of the OR is habituation on repeated presentation of the eliciting stimulus. It is suggested that if an ERP component is a component of the OR, it too will show a decrease in amplitude (habituation) on repeated presentation of the stimulus. It was suggested above that the processing reflected by the P3a appears to be related to an attentional switch resulting from detection of a mismatch between the features of the presented stimulus and those represented in the sensory memory trace (Naatanen and Gaillard, 1983; Naatanen, 1990). This is very similar to the eliciting conditions of the traditional OR components described above. If the P3a was a component of the OR it would be expected to decrease in amplitude as the eliciting stimulus is repeated.

Habituation of the P3a component over the first few presentations of the eliciting novel stimulus has been reported using stimuli in the auditory modality (Knight, 1984), the visual modality (Courchesne et al., 1975, 1978) and the somatosensory modality (Yamaguchi and Knight, 1990). These studies reported a decrease in amplitude of the P3a at frontal sites which was accompanied by an increase in amplitude of the P300 deflection at posterior sites. This shift from a frontal to a parietal distribution was thought to occur because the stimuli were no longer treated as 'novel' but were responded to in the same way as rare recognisable non-targets which show a P3 of parietal maximum (Courchesne et al., 1978). The habituation of the P3a supports the proposed involvement of its generator processes in the orienting of attention. No habituation of the target P3b has been reported in these studies.

The proposed involvement of the processes reflected by the P3a in the orienting of attention was investigated in the present experiment. The ERP studies discussed above reported rapid habituation of the P3a over the first few presentations of the novel stimuli. The present study investigated whether slow habituation occurred across a sequence of stimuli and whether dishabituation could be obtained by changing the eliciting stimulus. It was proposed that if the processes underlying the P3a are involved in classical orienting, changes in the OR would be expected to be reflected by changes in P3a amplitude, that is a decrease in amplitude with successive presentation of the stimulus and an increase in amplitude after a change to a different stimulus. As the P3b is elicited by significant target stimuli, it is predicted that it will not change in amplitude across the four blocks of trials.

METHOD

Subjects

Twelve healthy subjects (mean age 23, range 20-29 years, 5 female) were tested. All were paid volunteers.

Design

Subjects were presented with one sequence of 800 stimuli. The sequence consisted of the random mixing of a frequent 1000 Hz tone (P=0.7), a target 750 Hz tone (P=0.15) and a novel sound (P=0.15). A button press was required in response to the target tone. Two different novel sounds were used in the stimulus sequence. One novel sound was used as the rare non-target in the first 400 trials. It was,

therefore, possible to investigate whether the P3a elicited by the rare non-target decreased in amplitude (habituated) on repeated presentation of the stimulus. For the next 200 trials a different novel sound was presented as the rare non-target stimulus. Presentation of a different novel sound was included to see whether a recovery of P3a amplitude could be obtained. For the final 200 trials, the novel sound used in the first 400 trials was again presented as the rare non-target. Dishabituation of the P3a could, therefore, be investigated. Only one stimulus sequence was created and this was presented to all subjects.

Procedure

The experimental trials were preceded by a sequence of 15 practice trials which consisted of the random mixing of nine frequent tones, three target tones and three novel sounds. The practice trials were given to ensure that subjects were able to discriminate the tones so that the targets could be correctly detected. Approximately 2 minutes after successful completion of the practice trials, the experimental trials were presented. Stimuli were presented as eight blocks of 100 trials with a 1 minute break between blocks. Subjects were told that a sequence of stimuli would be presented which would consist mainly of a high tone with the occasional presentation of a low tone and another noise which was not a tone but sounded like an environmental noise. Subjects were instructed to press a button whenever they heard the lower of the two tones. Responses to the low tone were to be as fast as possible whilst avoiding mistakes. Subjects were told that as the stimulus sequence consisted of a large number of trials, it would be split into several blocks with a 1 minute break between each block.

DATA ANALYSIS

The grand average waveforms for the each block of 200 trials are shown in Figures 9.1a to 9.1d. Each waveform was produced by averaging the waveforms of 12 subjects.

Separate averages were obtained for each block of 200 trials for the target and novel sound stimuli. Averaging was carried out this way because it was predicted that these categories of stimuli would elicit P3b and P3a components respectively, the latter being thought to be related to the orienting response. As the orienting response is defined as showing habituation on repetition of the stimulus, it was predicted in the Introduction that changes in the P3a may occur across the blocks of trials. The waveforms elicited by the targets were averaged over a mean of 25 trials (range 14-30) in the first block of 200 trials, 27 trials (range 18-30) in the second block, 26 trials (range 12-30) in the third and 26 trials (range 13-30) in the fourth block. The waveforms elicited by the novel sounds were averaged over a mean of 24 trials (range 12-28) in the first block, 25 trials (range 14-30) in the second, 26 trials (range 15-30) in the third and 26 trials (range 13-30) in the fourth block. Only one average was obtained for the response to the frequent tones as a P300 would not be expected to occur in response to the stimuli in this condition. The waveform obtained in response to the frequents was averaged over a mean of 457 trials (range 316-546).

For the analyses, the frequents were assigned the label of condition 1. The targets and novel sounds were allocated a different condition number for each block of 200 stimuli. That is, in block 1 the targets were condition 2 and the novel sounds condition 3, in block 2 they were conditions 4 and 5, in block 3 conditions 6 and 7

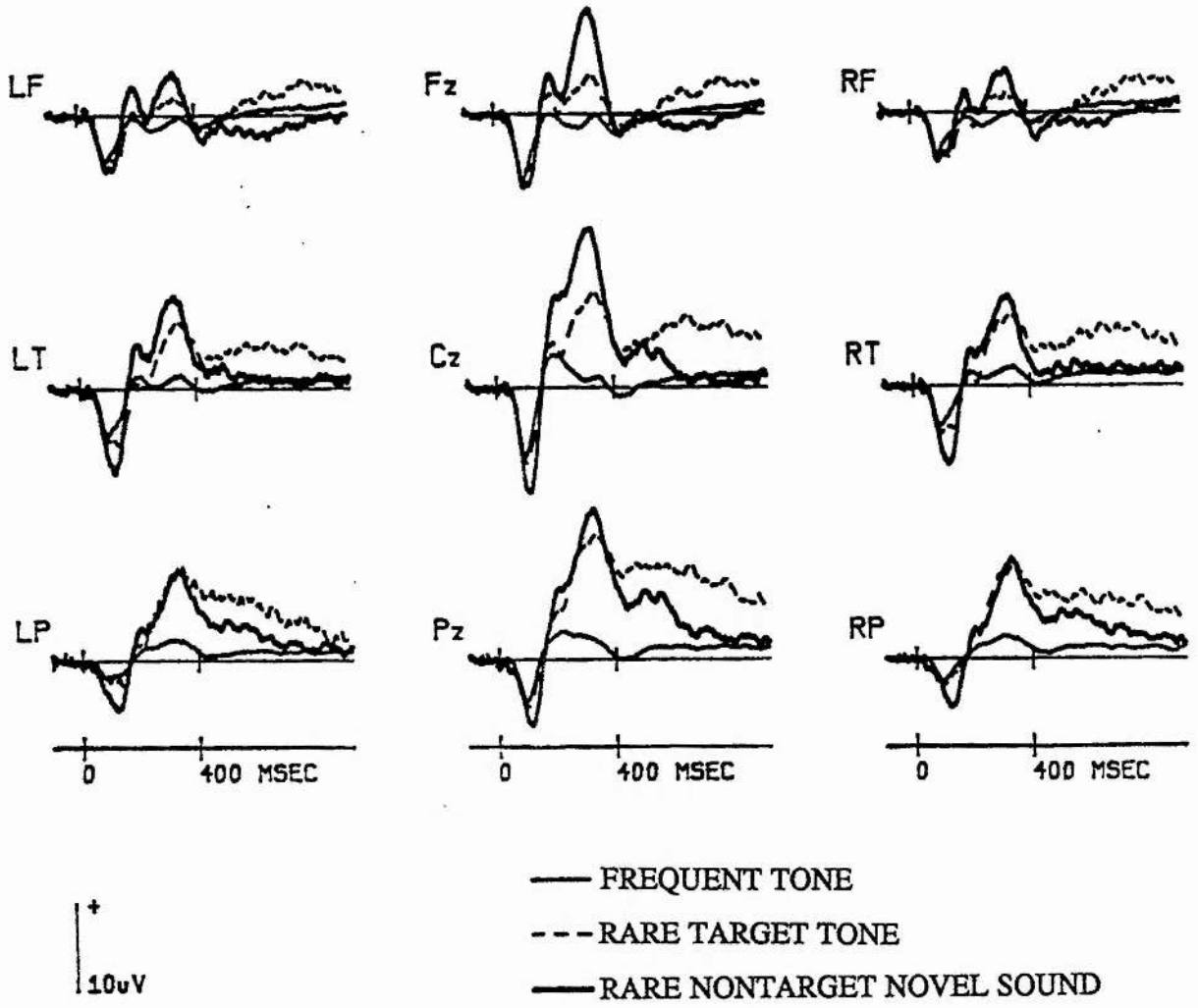


Figure 9.1a Waveforms elicited by frequent, target and rare nontarget stimuli, averaged over 12 subjects, for the first block of trials in experiment 6.

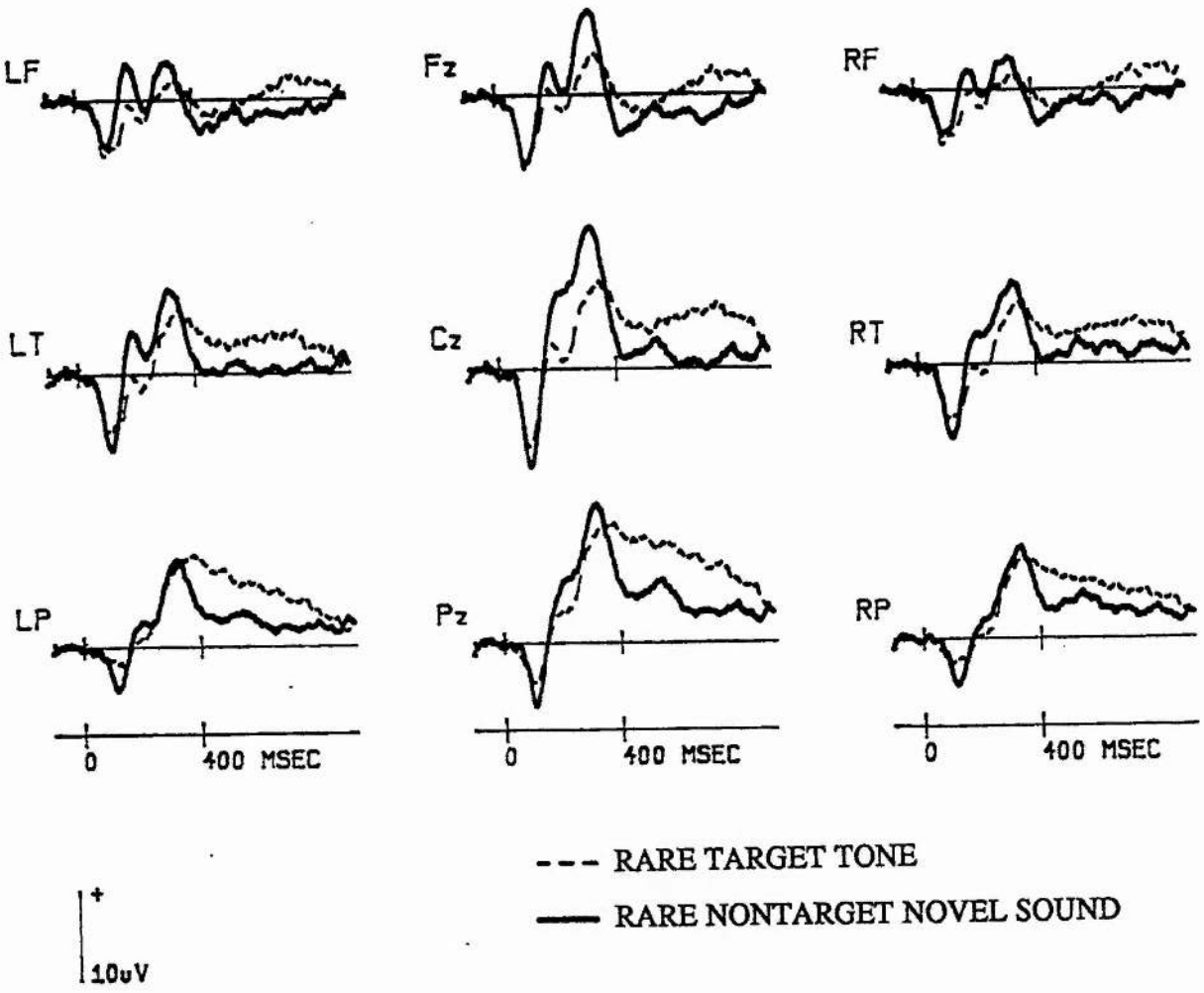


Figure 9.1b Waveforms elicited by target and rare nontarget stimuli, averaged over 12 subjects, for the second block of trials in experiment 6.

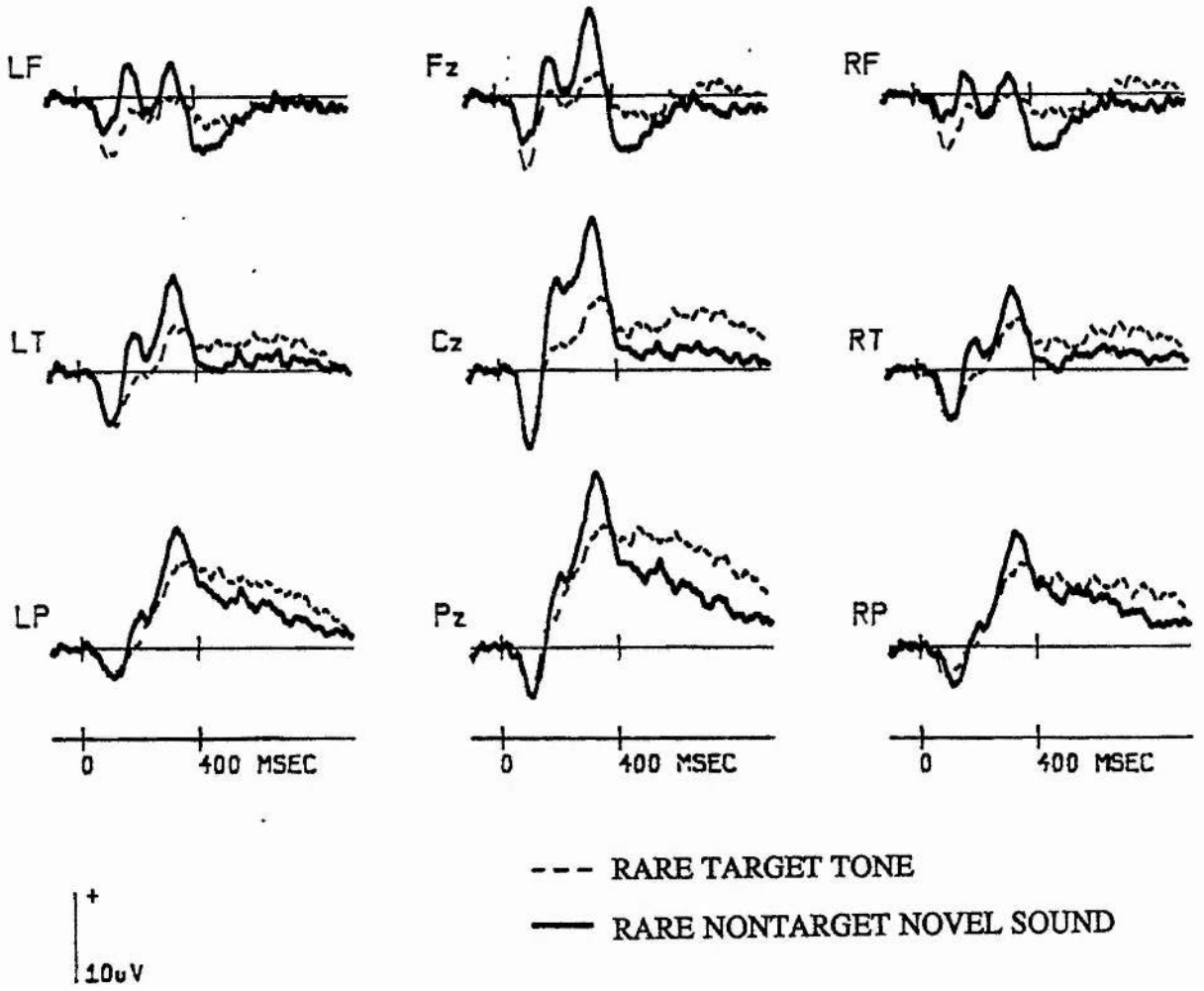


Figure 9.1c Waveforms elicited by target and rare nontarget stimuli, averaged over 12 subjects, for the third block of trials in experiment 6.

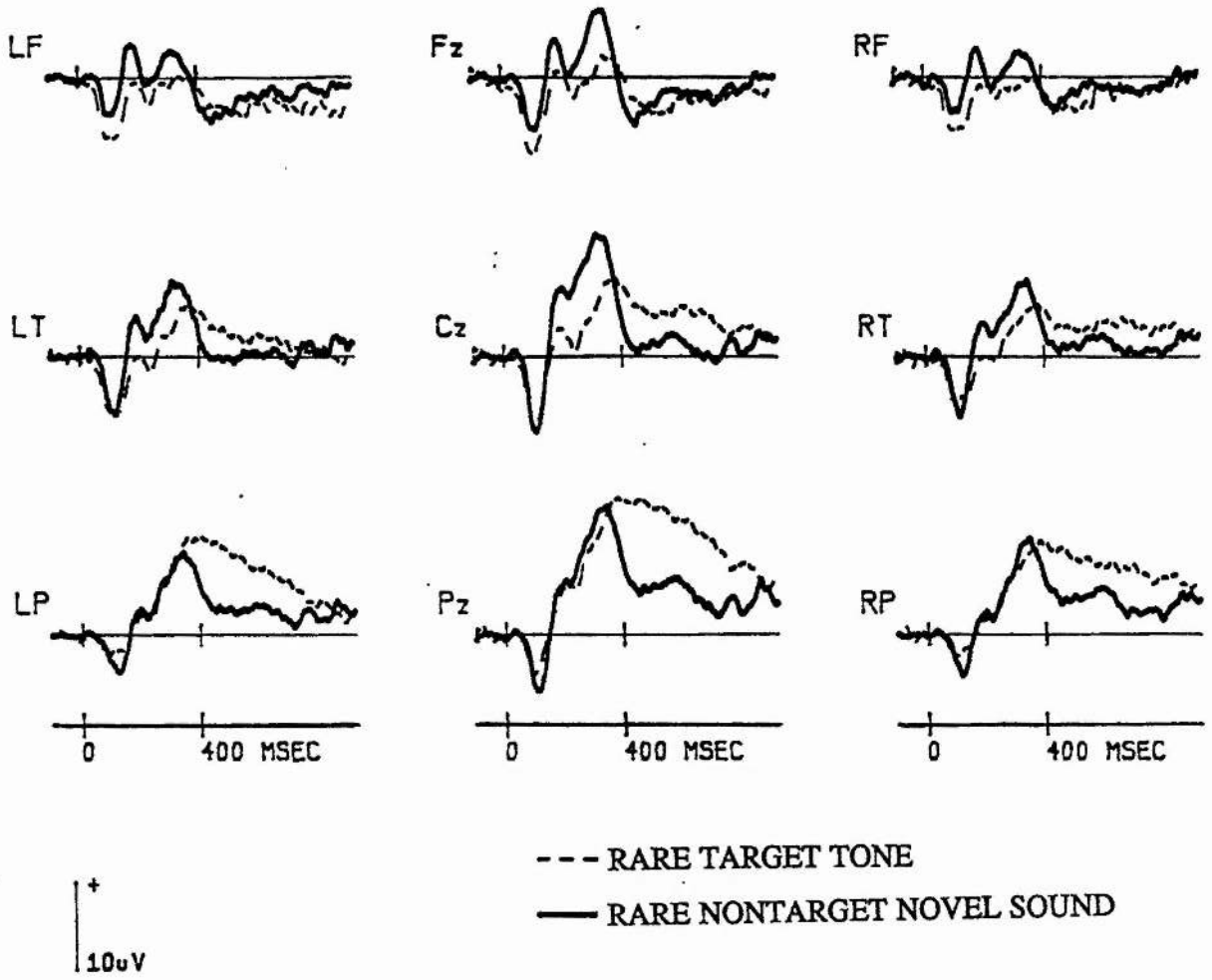


Figure 9.1d Waveforms elicited by target and rare nontarget stimuli, averaged over 12 subjects, for the fourth block of trials in experiment 6.

and in block 4 conditions 8 and 9 respectively. A total of nine conditions were therefore investigated in the experiment.

The peak latency of the N100 was measured for all rare stimulus conditions at Cz for all 12 subjects. For each subject the mean peak latency of the N100 across conditions was used to determine the latency window for the analysis of N100 amplitude. The P170 was measured at Fz in all rare conditions for 8 of the 12 subjects. The mean peak latency over the conditions was used to determine the latency window for investigating P170 amplitude. For the four subjects in whose waveforms it was impossible to measure a P170 peak, the mean peak latencies obtained from the other subjects were used to determine the latency window. The P300 deflection elicited by the targets (which will be referred to as the target P300) was measured at Pz in each block of 200 trials. It was possible to measure this P300 deflection in 8 of the 12 subjects. Separate latency windows were determined for each subject for each of the four blocks of 200 trials. For the 4 subjects in whose waveforms it was not possible to measure a P300 in response to the targets, the mean peak latency of this P300 measured in the waveforms of the other subjects was used to determine the latency window for each condition. The P300 elicited by the novel sounds (which will be referred to as the novel P300) was measured at Fz, Cz and Pz for each of the 12 subjects for each block of 200 trials. The mean peak latency of the P300 elicited by the novel sounds at the three electrode sites was used to determine the latency window.

The latency of the P300 deflection elicited by the novel sounds, at the three midline sites, was investigated by a 12*4*3 (subject*block*site) ANOVA. An 8*4*2 (subject*block*condition) comparison was made between the latency of the P300 deflection elicited by the targets and that elicited by the novel sounds at Pz. The

latencies of the N100 and P170 elicited by the targets and novel sounds were investigated by 12*4*2 and 8*4*2 (subject*block*condition) ANOVAs respectively. Repeated measures ANOVAs were used to investigate the amplitude differences between conditions. The ANOVAs took the form 12*4*2*3*3 (subject*block*condition*chain*site). The amplitude of the deflection elicited by the target was compared with that elicited by the novel sound for the P300, N100, P170 and 500-900 ms region. These analyses were performed before and after rescaling the mean amplitude data.

RESULTS

P300 before rescaling

Targets versus novel sounds

The P300 deflection elicited by the novel sounds was measured at Fz, Cz and Pz because in Experiment 1 the latency of this deflection was found to increase from anterior to posterior sites. An ANOVA comparing the latency of the P300 deflection elicited by the novel sound at the three midline sites showed no significant difference in latency across site. This was true for all four blocks of trials. As the P300 deflection elicited by the novel sounds did not differ significantly between site, the analysis comparing the latency of the P300 deflection elicited by the targets and novel sounds used the peak latency at Pz for both deflections. Pz was chosen as this was the site at which the P300 deflection elicited by the target had its maximum amplitude. The P300 deflection elicited by the targets was found to have a significantly longer latency than that elicited by the

novel sounds ($F(1,7)=20.43$, $P<0.005$). No significant main effect of block or interaction with block was found indicating that this latency difference was found for all blocks of trials. The mean latency of the P300 deflection elicited by the target, collapsed over block, was 363.4 ms and that of the novel sound 316.1 ms.

The results of the analysis of the amplitude data are shown in Table 9.1. No significant main effect of block was found. A significant main effect of condition was obtained indicating that the amplitude of the novel P300 was significantly larger than the target P300. Significant main effects of chain and site were also obtained.

A significant block by condition by chain interaction was obtained for which the corresponding means are plotted in Figure 9.2. The pattern of the means suggested that the amplitude of the novel P300 was larger in blocks 1 and 3 than in blocks 2 and 4, whereas the target P300 was larger in amplitude in blocks 1 and 2 than 3 and 4. Newman Keuls tests showed that these amplitude differences were not, however, significant. The three way interaction between block, condition and chain indicated that the difference in amplitude of the P300 between blocks differed across chain in a different way for each condition. The interaction was investigated by Newman Keuls tests comparing the difference in amplitude of the P300 between blocks, across chain, for each condition. For the novel sound the difference in P300 amplitude between blocks 1 and 2 and blocks 1 and 4 was larger at midline than at lateral sites and did not differ significantly between lateral sites. The difference in amplitude of the novel P300 between blocks 2 and 3 did not differ significantly between midline and left hemisphere sites but differed significantly between both these electrode chains and right hemisphere electrodes. The differences were larger at midline and left than at right hemisphere sites. The difference in novel P300 amplitude between blocks 3 and 4 was larger at midline than lateral sites and larger

Table 9.1. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli in each block of 200 trials, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.4,26.1	2.39	0.104
Condition (CC)	1,11	37.79	0.000*
Chain (CH)	2.0,22.0	29.06	0.000*
Site (ST)	1.1,11.7	35.16	0.000*
BL*CC	1.8,19.5	2.62	0.104
BL*CH	3.0,33.2	1.36	0.272
BL*ST	2.6,28.5	2.07	0.135
CC*CH	1.7,18.8	30.95	0.000*
CC*ST	1.6,17.6	14.43	0.000*
CH*ST	2.9,32.2	1.79	0.171
BL*CC*CH	3.4,37.9	3.56	0.019*
BL*CC*ST	2.2,23.7	1.48	0.249
BL*CH*ST	4.8,52.7	1.22	0.314
CC*CH*ST	1.8,20.3	6.16	0.009*
BL*CC*CH*ST	4.6,50.6	1.16	0.343

RESCALED AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.2,24.6	0.04	0.968
Condition (CC)	1,11	0.39	0.543
Chain (CH)	2.0,22.0	28.82	0.000*
Site (ST)	1.1,11.7	35.35	0.000*
BL*CC	1.9,20.4	0.51	0.595
BL*CH	2.9,32.0	1.14	0.349
BL*ST	2.7,29.3	0.46	0.687
CC*CH	1.6,18.0	31.35	0.000*
CC*ST	1.6,17.5	13.62	0.001*
CH*ST	2.9,32.1	1.72	0.185
BL*CC*CH	3.9,42.8	0.46	0.761
BL*CC*ST	2.3,25.0	0.42	0.684
BL*CH*ST	4.7,51.7	0.98	0.432
CC*CH*ST	1.9,20.8	5.74	0.011*
BL*CC*CH*ST	4.5,49.3	1.09	0.375

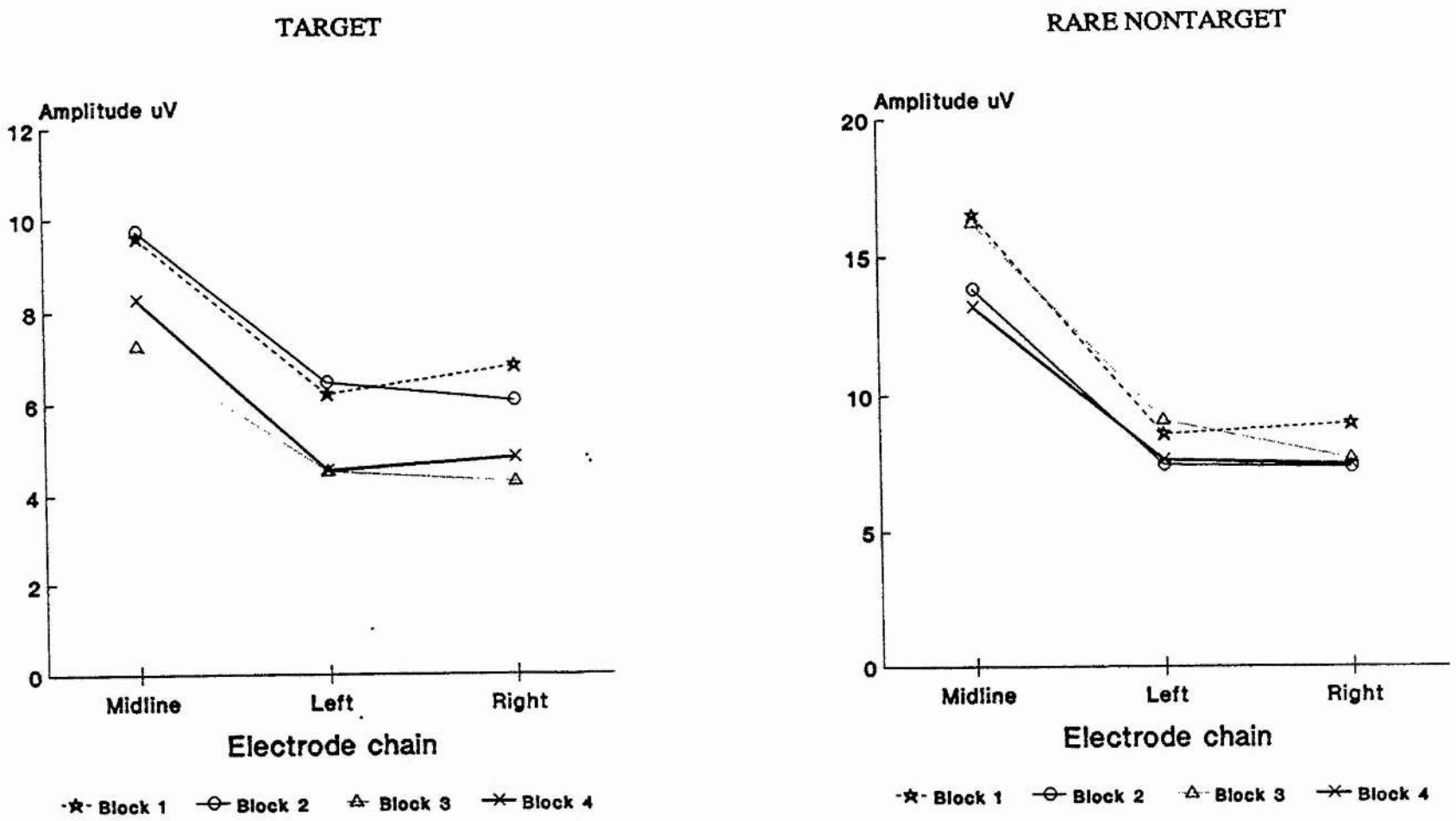


Figure 9.2 Graphs illustrating the amplitude of the P300 deflection elicited by the two categories of rare stimuli at each electrode chain (collapsed over site) for each block of trials in experiment 6.

at left than right hemisphere sites. The difference in novel P300 amplitude between blocks 2 and 4 did not differ significantly across chain. The difference in amplitude between blocks 1 and 3 did not differ significantly between midline and lateral sites but differed significantly between left and right hemisphere sites, being larger at left than right hemisphere sites. For the target P300 the differences in amplitude between blocks did not differ significantly between chains.

Significant interactions were found between condition and chain, and condition and site. A significant three way interaction was found between condition, chain and site which will be discussed in relation to the analysis of the rescaled data.

A 12*4*3*3 (subject*block*chain*site) ANOVA was performed on the novel P300 amplitude data to investigate any changes in amplitude across block which may not have been seen in the ANOVA comparing the two rare conditions. No significant main effect of block was obtained. A significant interaction was obtained between block and chain. Newman Keuls tests showed no significant difference in amplitude between block at any electrode chain. Inspection of the mean amplitudes suggested that the amplitude of the P3a was larger in blocks 1 and 3 than blocks 2 and 4. Newman Keuls tests comparing the difference in amplitude between blocks 1 and 2, 1 and 4, 3 and 2 and 3 and 4 across chain showed that the interaction was obtained because the amplitude differences were larger at midline than lateral sites.

P300 after rescaling

Targets versus novel sounds

Table 9.1 shows significant main effects of chain and site. A significant interaction was found between condition and chain because the novel P300 was distributed significantly more over midline sites than the target P300. A significant condition by site interaction was found because the novel P300 was distributed maximally over central and parietal sites, whereas the target P300 was distributed maximally over parietal sites. A three way interaction was found between condition, chain and site (see Figures 9.3a, 9.3b, 9.3c). The interaction was investigated by Newman Keuls tests comparing the difference in rescaled amplitude between the P300 elicited by the target and novel sounds, across site, for each electrode chain. At midline sites a larger difference in the rescaled P300 amplitude elicited by targets and novel sounds was found at central and frontal sites than at parietal sites. The difference in rescaled P300 amplitude between targets and novel sounds did not differ significantly between central and frontal sites. The novel P300 was distributed more over frontal and central sites than the target P300 but did not differ from the target P300 at Pz. Over the left hemisphere, the difference in amplitude of the P300 elicited by the targets and novel sounds did not differ between frontal and central sites but differed significantly between these sites and parietal sites. There was no difference in P300 elicited by the two categories of rare stimuli at frontal and central sites but the target P300 was distributed more over the left parietal site than the novel P300. Over the right hemisphere the difference between P300 elicited by targets and novel sounds did not differ significantly across site.

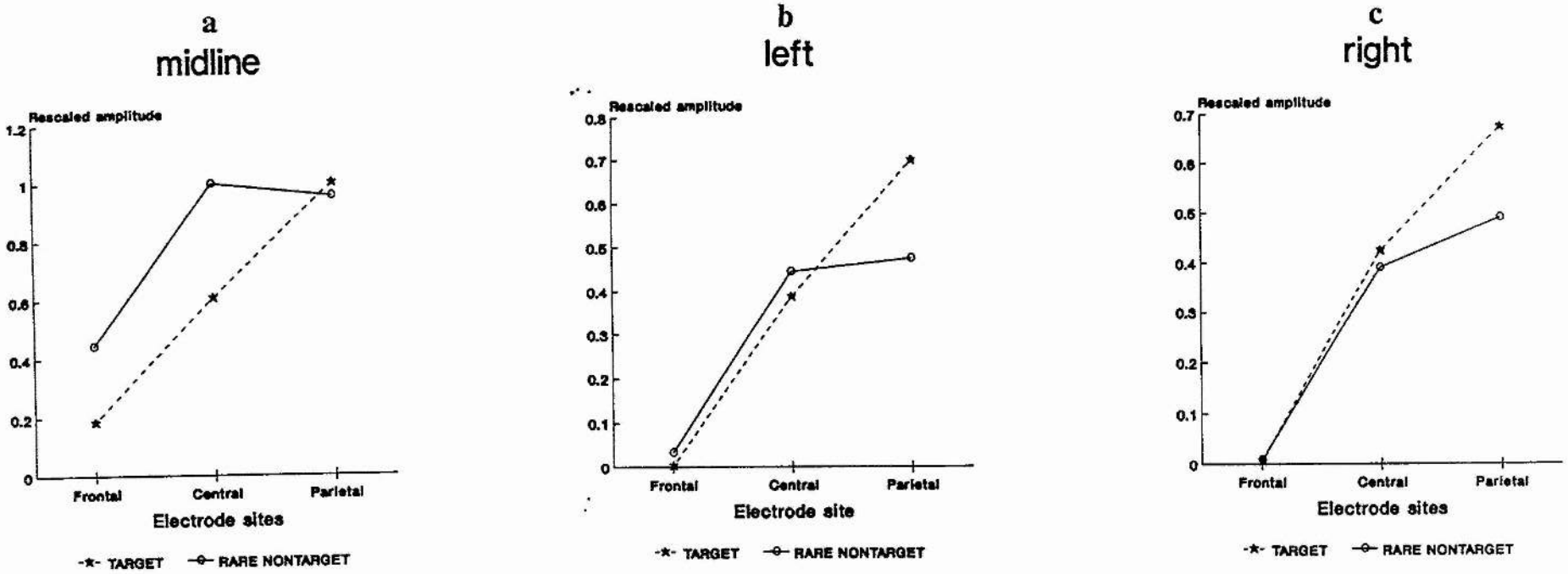


Figure 9.3 Graph illustrating the distribution of rescaled amplitude of the P300 deflection over (a) midline sites, (b) left hemisphere sites and (c) right hemisphere sites, for the two categories of rare stimuli in experiment 6.

N100 before rescaling

The latency of the N100 deflection was found not to differ significantly between conditions or between the four blocks of trials. The mean latencies of the N100, collapsed over block, were 108.3 ms and 109.1 ms for the targets and novel sounds respectively.

Table 9.2 of the Appendix shows the results of the analysis of the amplitude data. No significant main effect of block was found on the amplitude of the N100 and no significant interactions with block were obtained. Table 9.2 of the Appendix shows a significant main effect of chain which was obtained because the N100 deflection had a maximum amplitude at midline sites. A significant main effect of site was obtained which interacted significantly with condition. Newman Keuls tests showed no significant differences in amplitude between the two conditions at any site. The interaction provides important information concerning the scalp distribution of the N100 and so will be discussed in relation to the analysis of the rescaled N100 amplitude data.

N100 after rescaling

Table 9.2 of the Appendix shows a significant main effect of chain in the analysis of the rescaled N100 amplitude data. The effect confirmed the midline distribution of the N100 suggested by the analysis of the raw amplitude data.

As for the analysis of the raw amplitude data, a significant main effect of site was obtained which interacted significantly with condition. Newman Keuls tests comparing the rescaled amplitude of the N100 across site for each condition showed

that the N100 elicited by the targets was significantly more negative at frontal and central than at parietal sites but showed no difference in amplitude between frontal and central sites. The N100 elicited by the novel sounds was significantly more negative at central than at parietal and frontal sites which did not differ significantly. That is the N100 elicited by the target tones had a fronto-central maximal distribution, whereas that elicited by the novel sounds had a central maximal distribution.

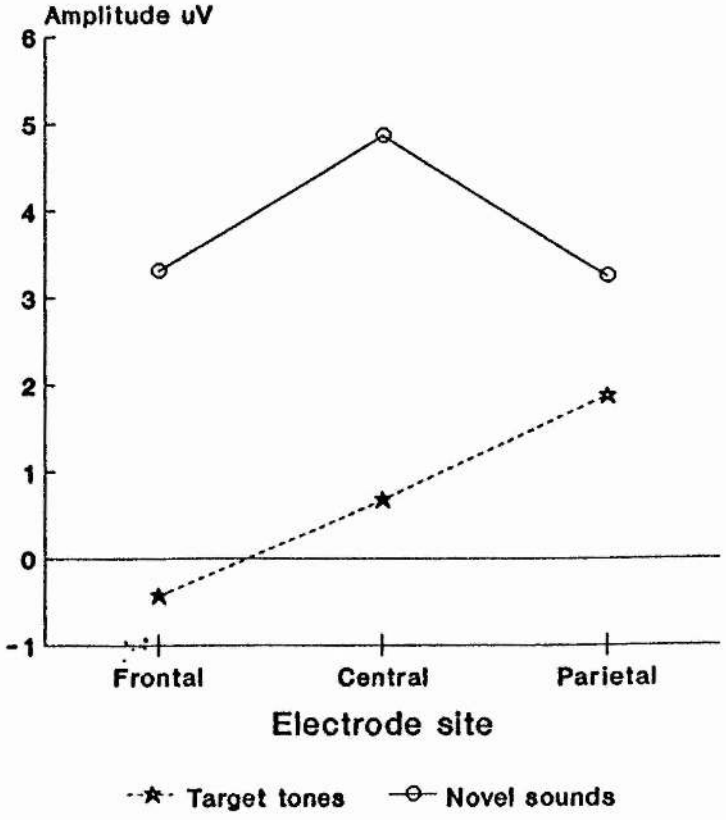
P170 before rescaling

The P170 deflection elicited by the targets was found to have a significantly longer latency than that elicited by the novel sounds ($F(1,7)=6.491$, $P<0.005$). No significant main effect or interactions with block were obtained, suggesting that this latency difference was found for all four blocks of trials. The mean latencies of the P170, collapsed over block, were 196.8 ms and 186.5 ms for the targets and novel sounds respectively.

The results of the analysis of the P170 amplitude data are given in Table 9.3 of the Appendix. It can be seen that no significant main effect of block was found on P170 amplitude and no significant interactions were found with block. Significant main effects of condition and chain were obtained. The main effect of condition was obtained because the P170 elicited by the novel sound was significantly larger in amplitude than that elicited by the target tone.

Table 9.3 of the Appendix shows a significant interaction between condition and site (see Figure 9.4). Newman Keuls comparison of the amplitude of the P170 across site for each condition showed that the P170 elicited by the target was significantly

Figure 9.4 Graph illustrating the amplitude of the P170 elicited by the two categories of rare stimuli at each electrode site in experiment 6 (collapsed over the four blocks of trials and over the chains of electrodes).



larger at parietal than at frontal sites but did not differ significantly between frontal and central or central and parietal sites. In contrast, the amplitude of the P170 elicited by the novel sound did not differ significantly across site. Newman Keuls tests were also performed comparing the difference in amplitude of the P170 elicited by the targets and novel sounds across site. The difference in P170 elicited by targets and novel sounds did not differ significantly between central and frontal sites but was significantly different at both from the difference between conditions at parietal sites. The difference in amplitude between conditions was larger at frontal and central sites than at parietal sites.

A significant chain by site interaction was obtained which will be discussed in relation to the rescaled data.

P170 after rescaling

Table 9.3 of the Appendix shows significant main effects of chain and site. No significant main effect or interactions with condition were found. A significant chain by site interaction was obtained. A Newman Keuls test was used to compare the rescaled P170 amplitude across chain for each site, collapsed over condition. At frontal sites there was no significant difference in P170 rescaled amplitude across chains. At central and parietal sites P170 was larger at midline than at lateral sites which did not differ. A comparison of rescaled P170 amplitude across site for each chain, showed that at the midline the P170 was larger at parietal and central than at frontal sites, whereas over lateral electrode chains there were no differences between sites.

500-900 ms region before rescaling

Table 9.4 of the Appendix shows a significant main effect of condition because the amplitude of the 500-900 ms region elicited by the targets was significantly larger than that elicited by the novel sounds. Significant main effects of chain and site were also found. Significant interactions were found between block and site, and block, condition and site (see Figure 9.5a and 9.5b). The three way interaction was investigated by comparing the difference in amplitude between block of the 500-900 ms region across site for the two categories of rare stimuli. For the targets the difference in amplitude between block 1 and block 2 did not differ significantly across site. The differences, of the target 500-900 ms region, between block 1 and block 3 and block 1 and block 4 were larger at frontal than at parietal and central sites and larger at central than at parietal sites. The difference, of target 500-900 ms region, between block 2 and block 3 was larger at frontal than at parietal sites but did not differ between central and parietal sites or frontal and central sites. The differences were obtained because at frontal sites the 500-900 ms region decreased in positivity from block 1 to block 4, showed a smaller decrease across block at central sites and no change at parietal sites. The 500-900 ms region elicited by the novel sound did not differ in amplitude between blocks.

Significant condition by chain and chain by site interactions were obtained. A significant three way interaction was obtained between condition, chain and site. This three way interaction was investigated by Newman Keuls tests comparing the difference in amplitude of the 500-900 ms region between chains across site for each condition. For the targets the difference in amplitude between midline and left, and midline and right electrode chains was larger at parietal and central sites than at frontal sites and larger at parietal than at central sites. The difference in amplitude

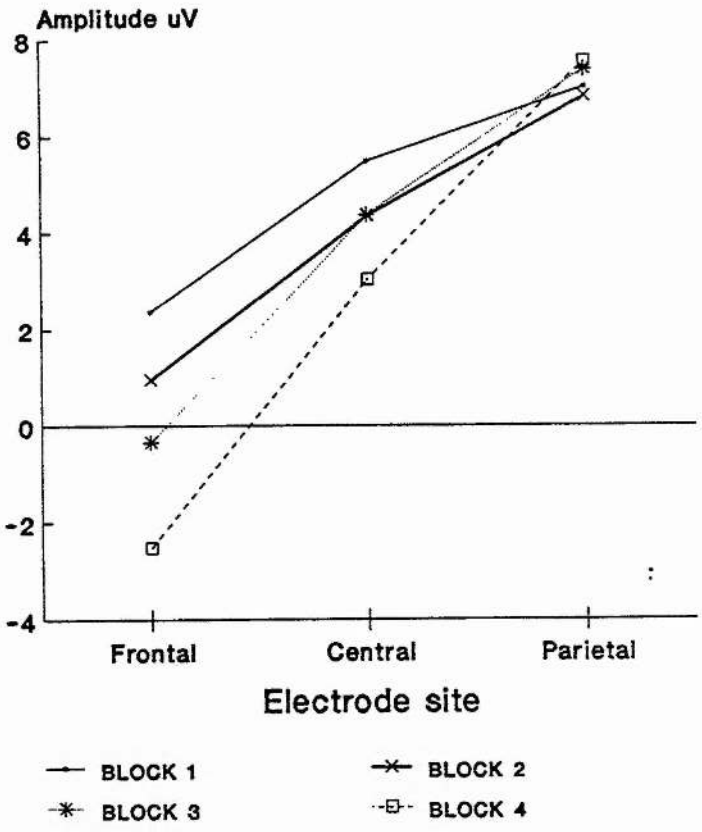


Figure 9.5a Graph illustrating the amplitude of the 500-900 ms region elicited by targets at each site (collapsed over electrode chain) for each block of trials in experiment 6.

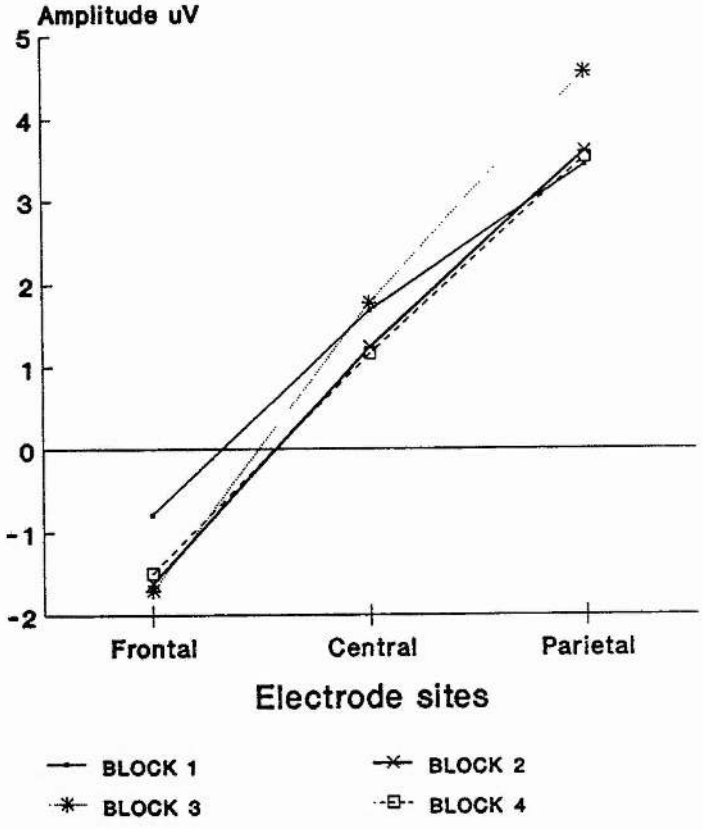


Figure 9.5b Graph illustrating the amplitude of the 500-900 ms region elicited by rare nontargets at each site (collapsed over electrode chain) for each block of trials in experiment 6.

Figure 9.6 Graph illustrating the distribution of the 500-900 ms region, across site, for each electrode chain in experiment 6 (collapsed over blocks of trials and condition).

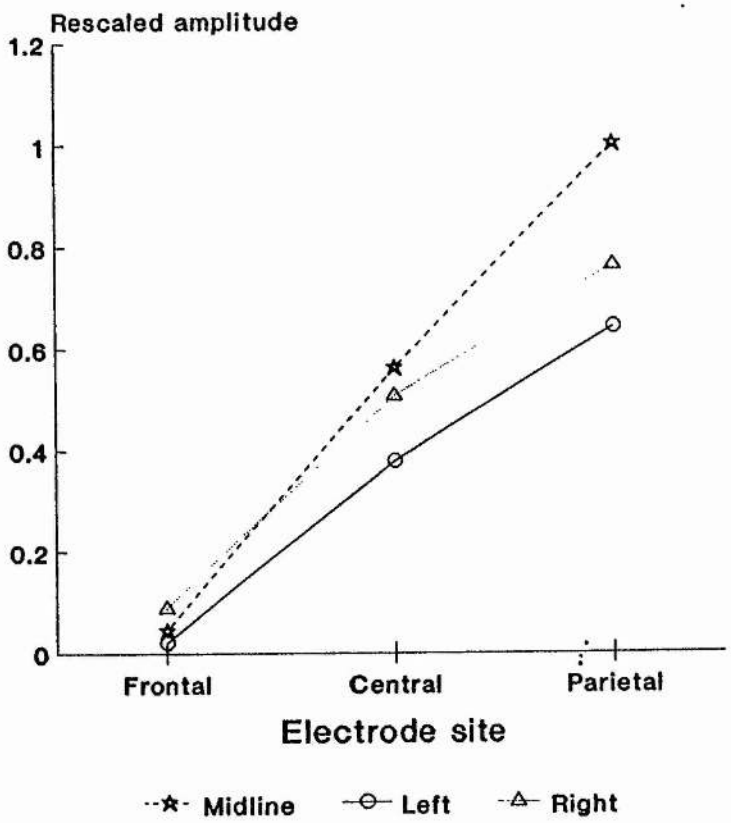


Table 9.5 Mean reaction time (msec) for the response to the rare target stimulus, mean number of hits for each block of the task and the mean number of false alarms collapsed over the four blocks of trials for the auditory oddball task of experiment 6.

	MEAN	SD
BLOCK 1		
Reaction time	477.2	95.4
No. hits	29.6	0.7
BLOCK 2		
Reaction time	517.3	114.5
No. hits	29.9	0.3
BLOCK 3		
Reaction time	521.3	127.6
No. hits	29.7	0.7
BLOCK 4		
Reaction time	510.9	118.2
No. hits	29.8	0.6
OVERALL		
No. false alarms	1.8	1.3

between right and left lateral chains showed no significant differences between sites. For the novel sounds the difference between midline and right and midline and left electrode chains was larger at parietal than at frontal and central sites but did not differ significantly between central and frontal sites. The difference between right and left electrode chains showed no significant differences between sites.

500-900 ms region after rescaling

Table 9.4 of the Appendix shows significant main effects of chain and site. A significant chain by site interaction was obtained (see Figure 9.6). The interaction was investigated by comparing the difference in rescaled amplitude of the 500-900 ms region between chains, across site. The difference between midline and right, and midline and left, electrodes was significantly larger at parietal than at frontal sites but no significant differences were found between central and frontal sites or central and parietal sites. The difference in amplitude between right and left electrode chains showed no significant differences across site.

Behavioural Data

Behavioural data is summarised in Table 9.5. No significant difference in reaction time to respond to the target tone was found between blocks ($F=0.37$, $P>0.05$).

Summary of results

As in experiment 1, the target tones elicited a parietally distributed P300 deflection (P3b), whereas the rare nontarget novel sounds elicited an earlier, more anteriorly distributed deflection (P3a). The amplitude of the P3a and P3b did not differ

significantly between the four blocks of trials. The trend of the mean amplitude of the P3a, however, over the blocks of trials was in the predicted direction. There was a decrease in amplitude from block 1 to block 2 and an increase in amplitude in block 3, the amplitude of the P3a in block 4 did not differ from that in block 2. As in experiment 1, an N100 with a central maximum was elicited by the novel sounds and a fronto-centrally distributed N100 elicited by the target tones. For both categories of rare stimuli the N100 was maximally distributed over midline sites. The P170 elicited by the novel sound was larger in amplitude than that elicited by the target tones. The amplitude of the N100 and P170 elicited by both target tones and novel sounds did not change between the four blocks of trials. As in experiment 1, the 500-900 ms region was found to be distributed maximally over the midline at parietal sites but to be distributed evenly over electrode chains at frontal sites. The amplitude of the 500-900 ms region became less positive from block 1 to block 4 at frontal sites, showed a small decrease in positivity at central sites but did not change in amplitude between block at parietal sites.

DISCUSSION

P300

As in Experiment 1, the target tones elicited a P300 deflection which was distributed maximally over parietal sites. This deflection was considered to be reflecting the contribution to the waveform of the P3b component. The novel sound elicited a P300 deflection which, as in Experiment 1, had a centro-parietal maximum. In Experiment 1 this deflection was labelled the P3a to indicate that an anteriorly distributed P3a component was contributing to the waveform which was not present

in the waveforms elicited by the targets. In the present experiment, as in Experiment 1, the latency of the P300 deflection elicited by the novel sounds was found to be significantly shorter than that elicited by the target. This latency difference indicates further the contribution of a P3a component to the P300 deflection elicited by the novel sounds, as previous studies have reported the P3a to have an earlier latency than the P3b. The evidence from latency data, for this claim, is only weak. The latency difference could have been produced because the process reflected by the P3b occurred earlier in response to the novel sounds because perhaps they were easier to discriminate from the frequent stimuli than the target tones. The amplitude results of the present experiment showed that a single novel sound, presented as the rare non-target among frequent and target tones, elicited a P3a which did not differ from that elicited by the 30 different novel sounds presented as rare non-targets in Experiment 1. This finding indicates that in order to elicit a P3a the stimulus does not have to be novel in the sense that it has never been heard before but instead suggests that the extent to which it deviates from other stimuli in the sequence or its attention capturing nature may be more important determinants of P3a elicitation. As in Experiment 1, the frequent stimuli did not elicit a P300 deflection.

The main prediction being investigated in the present experiment was that the P3a, elicited by the novel sound, would show a decrease in amplitude (habituation) with increasing number of presentations of the novel sound, that is, it was predicted that there would be a decrease in amplitude from the first to the second block of 200 trials. It was predicted that changing the rare non-target to a different novel sound would cause a P3a to be elicited which was of the same amplitude as that originally elicited by the first novel sound. The final prediction was that subsequent presentations of the first novel sound would produce a P3a of similar amplitude to that elicited in the first block of trials (dishabituation). The results of the analysis on

the P300 amplitude data showed a significant block by condition by chain interaction. Inspection of the mean amplitudes showed changes in P3a amplitude between blocks which were consistent with the predictions. The P3a decreased in amplitude at all electrode chains from the first to the second block of trials and increased to an amplitude equivalent to that elicited in the first block when a different novel sound was presented (block 3). Contrary to the predictions, a decrease in amplitude was seen from block 3 to block 4. Newman Keuls post hoc tests showed that these changes in amplitude between the blocks of trials, however, were not significant. This was true even when an ANOVA was performed only on the P3a data. The trend of the means suggested that the amplitude of the P3b component changed across the blocks of trials in a different way to the P3a. The P3b elicited in blocks 1 and 2 was larger in amplitude than that elicited in blocks 3 and 4. As for the P3a, post hoc testing showed that these amplitude changes were not statistically significant.

The small changes in amplitude across block of the novel P300 were found to be larger at midline than at lateral sites. This distribution of the changes suggests that it was reflecting the change in amplitude of a component distributed maximally over the midline. The P3b component elicited by the target tone has been shown, in experiment 1, to be distributed evenly over all three electrode chains. The change in amplitude of the P300 deflection elicited by the novel sound is, therefore, unlikely to be due to a change in amplitude of an overlapping P3b component. If this were the case then equivalent changes would have been seen at all three electrode chains, as was found for the amplitude changes across block of the P3b elicited by the target tones. The changes in amplitude of the P300 deflection elicited by the novel sound, across block, therefore appeared to be due to changes in amplitude of the P3a component.

Although the trend of the mean amplitude of the P3a is suggestive of habituation, the finding that this amplitude change was not statistically significant and the absence of dishabituation following stimulus change suggests that the P3a is not a component of the OR. This does not necessarily imply that the P3a is not related in some way to the OR. It is possible that the P3a reflects a process which is related to, or necessary for, the OR but, unlike the autonomic nervous system changes described in the Introduction, is not actually a component of this reflex. The P3b component also showed a change in amplitude across the four blocks of trials but again this was not statistically significant. It is therefore suggested that, as the P3a and P3b showed only a small decrease in amplitude on repetition of the respective stimuli, they can not be considered to be components of the OR which traditionally habituate to extinction. The OR literature, however, suggests that the OR to significant stimuli does not habituate. It is possible that both the rare non-target and target stimuli are treated as significant stimuli in the present task and correspondingly there is no habituation of the OR elicited by them. In the present experiment it could therefore be suggested that the P3a and P3b are components of the OR but that they do not habituate because the stimuli are treated as significant.

The orienting response is thought to result from the mismatch between a presented stimulus and a neuronal model or schema which contains the subjects knowledge of the situation. Naatanen (1990) has suggested that the neuronal model against which this mismatching process occurs represents the physical features of recently occurring stimuli in a task. Sokolov, however, has a broader view of the neuronal model suggesting that it additionally represents information such as associated behavioural responses and contextual information. It is unlikely that the physical features of the rare target tones and novel sounds would be represented in sensory

memory when the next stimulus of that category is presented. The low probability with which these stimuli occurred would have prevented reinforcement and maintenance of the trace (Naatanen, 1990). According to Naatanen's model the target and rare non-target stimuli should have continued to mismatch the sensory memory trace of the frequent stimulus throughout the task and so no decrease in amplitude of these components would have been expected. The finding of the present experiment that there was no statistically significant decrease in P3a and P3b amplitude between blocks of trials is therefore consistent with Naatanen's theory. Naatanen suggests that the P3a is not actually a component of the OR but reflects a process related to the attention switch. It would be possible for a P3a to occur, reflecting a call for attention, without the OR necessarily being triggered.

It is possible that, for both the P300 and the other deflections to be discussed below, large changes in amplitude occurred over the first few presentations of the stimulus, possibly even during the practice trials, and then remained at a fairly stable level on subsequent presentations of the stimulus. The averaging procedure used in the present experiment did not allow the investigation of this possibility but it was investigated in a systematic manner in a subsequent experiment (see Experiment 7 (Chapter 10)).

N100

Both the target tone and the rare non-target novel sound elicited an N100 deflection which was maximally distributed over midline sites. As in Experiment 1, the targets elicited an N100 which was distributed maximally over frontal and central sites whereas the novel sound elicited an N100 which was distributed maximally over central sites. The difference in scalp distribution of the N100 elicited by the two

categories of rare stimuli in Experiment 1 was not therefore due to the rare non-targets being a heterogeneous set of novel sounds compared with the targets which were a single tone. No change in amplitude of the N100 was found over the four blocks of trials. As discussed with reference to the P300 deflection, changes in amplitude may have occurred within the first block of trials but would have been lost due to averaging. The results from the present experiment suggest that the N100 does not habituate on repeated presentation of the stimulus and so is not a component of the OR.

P170

As in Experiment 1, a P170 deflection was present in the waveforms elicited by both categories of rare stimuli. This deflection was of larger amplitude in response to the novel sounds than the targets. The difference in latency of the P170 elicited by the targets and novel sounds may be reflecting the differing contributions of the P165 and P200 components in the two conditions. The distribution of the P170 across site did not differ significantly between conditions. For both conditions the distribution of the P170 across site differed between electrode chains. At the midline the P170 showed a centro-parietal maximum whereas no differences between site were found laterally. The difference in P170 amplitude between electrode chains was larger at central and parietal sites than at frontal sites. The apparent scalp distribution of the P170 is due to its superimposition on the P300 deflection which, as discussed in the previous experiments, makes interpretation of the P170 difficult. No changes in amplitude of the P170 were found between the four blocks of stimuli. This finding can be interpreted in the same way as for the N100.

500-900 ms region

As in Experiment 1, the region of waveform from 500-900 ms, elicited by both categories of rare stimuli, was found to be more positive at parietal than frontal sites. This region of the waveform elicited by the targets was found to decrease in positivity at frontal sites over the four blocks of trials. A small decrease in positivity across blocks was found at central sites but no change in amplitude between the four stimulus blocks was found at parietal sites. This finding provides further support for the dissociation of the slow wave since repeated presentation of a target stimulus appears to affect the amplitude of the frontal slow wave but not affect the amplitude of the posterior slow wave. An alternative interpretation is, however, that over the course of the stimulus sequence there is a build up of an overlapping frontal negativity. The amplitude of the 500-900 ms region of the waveform elicited by the rare non-target novel sound did not differ significantly across block at any electrode site. The difference between the targets and novel sounds in the way in which the amplitude of the 500-900 ms region differed across blocks suggests that for the target a process may become active on repeated presentation of the targets which is not active on repeated presentation of the novel sounds. The nature of this process is uncertain.

Behavioural data

The number of hits and number of false alarms suggest that the subjects were performing at ceiling level throughout the task.

Summary

The main conclusion to be drawn from the results of the present experiment was that the P3a elicited by the rare non-target novel sounds and the P3b elicited by the target tones did not habituate significantly over subsequent presentations of the respective stimuli. This suggests that neither the P3a nor the P3b are direct reflections of the OR. This does not, however, imply that they do not reflect processes related to or necessary for the OR.

CHAPTER 10

EXPERIMENT 7: EFFECT OF LOCAL STIMULUS SEQUENCE ON THE P3A

INTRODUCTION

The mismatch negativity (MMN) is a negative deflection in the waveform which occurs in response to a change of stimulation. Two theories offer explanations for the occurrence of the MMN. The first of these proposes that one set of neurones is responsive to a particular stimulus. If this stimulus is presented many times the neurones become refractory and no longer respond. On the presentation of a different stimulus a different group of neurones is activated which causes the production of the MMN. The alternative theory proposes that on repeated presentation of a stimulus a representation of the stimulus forms in sensory memory. If a different stimulus is then presented, an automatic comparison occurs between the features of the incoming stimulus and those represented by the neuronal trace. If a match does not occur the process reflected by the MMN is elicited. Naatanen (1990) suggested that the memory trace hypothesis was the most likely explanation. This suggestion was made on the basis of evidence from a number of studies including reports of MMNs in response to decreases in intensity and increments and decrements in duration. These examples are all instances in which the change would not be expected to activate a different group of neurones. In the study of Winkler et al. (in prep), subjects were presented with a frequently occurring stimulus which consisted of simultaneously presented 600 and 700 Hz tones. The rare stimulus was one of the two tones alone (with intensity equalised to that of the frequent stimulus). Both deviant stimuli elicited an MMN. As the neurones responsive to both frequencies of rare stimuli would have been activated by the frequent stimulus, the

result of partial stimulus omission is difficult to explain in terms of the activation of a new set of neurones.

The MMN is followed by another negative component, the N2b, and a positive component, the P3a. These components are elicited by deviant stimuli more readily if the sequence of stimuli is being attended than if it is being ignored, however if the rare stimuli in an ignored sequence are very deviant from the frequent stimulus, the N2b and P3a are elicited. The P3a has been proposed by Naatanen (1990) to be an indicator of an attentional switch from preattentional processing to attentional processing leading to "conscious discrimination" of the stimulus (i.e. processing which produces results which are available for conscious report). The attentional switch is produced only if a mismatch is detected between the features of the stimulus and those represented in the passively held neuronal traces of sensory memory. In order for the attentional switch to occur, the N2b process has to be activated above a certain threshold. The strength of the N2b generator process depends on the size of the mismatch which is determined both by the strength of the trace in sensory memory and the deviance of the presented stimulus from the trace. Rarely presented stimuli are more likely to gain access to attentional processing if the task requires the sequence of stimuli to be attended because in this situation a "facilitatory coupling" is set up between the N2b and MMN processes. It is proposed that as the strength of the attentional switch is dependent on the size of the mismatch, changes in the magnitude of the mismatch (reflected by the amplitude of the MMN) will produce corresponding changes in the strength of the process underlying the attentional switch (reflected by P3a amplitude).

Naatanen (1990) suggests that the passively formed sensory memory trace, against which the mismatch detecting comparison process occurs, has a duration of only 5-

10 s. The short duration of this sensory memory trace was suggested by the finding that the MMN did not show long term habituation and by the results of studies manipulating the inter-stimulus-interval until an MMN no longer occurred (see Naatanen, 1990). If the duration of the sensory memory trace is short, it would be predicted that the elicitation and amplitude of the MMN would only be affected by relatively recent stimuli in the sequence. It has been shown (Sams et al., 1984) that after the repetition of a particular stimulus, the presentation of a stimulus which does not match the sensory memory trace (to be referred to here as a deviant stimulus) elicits an MMN. Sams et al. (1984) showed that if the deviant stimulus was immediately followed by the same deviant stimulus, the MMN produced was larger on the first than on the second presentation of the deviant stimulus. This decrease in MMN amplitude on immediate repetition of the deviant stimulus was proposed to occur because a trace of the deviant stimulus would have still been present in sensory memory when the second stimulus was presented. When one of the stimuli which had been repeated many times previously (a frequent) was then presented, it also produced a small MMN (mismatching against the trace of the deviant stimulus still present in sensory memory). However, the response, was small because a trace of the frequent stimulus would have still been present in sensory memory. As the occurrence of the P3a appears to be dependent on the occurrence of the MMN, it is proposed in the present experiment that the P3a will also be affected by the local sequence of stimuli.

A number of hypotheses concerning the elicitation of the P3a can be proposed on the basis of the findings of research investigating the MMN.

The first suggests that the initial stimulus of a sequence will not produce a P3a, even if it is novel or unrecognisable. This is because no strong or stable representation

will be present in sensory memory against which a mismatch could occur and hence no MMN and subsequent P3a will be elicited. It could be argued that there is always a representation present in sensory memory against which a comparison could be made, however, if prior to the presentation of a novel stimulus the subject is presented with constantly changing stimulation, the representations in sensory memory will only be weak and so only small mismatches will occur which may be insufficient to cause an attentional switch. The absence of an MMN and N2b-P3a does not imply that an OR does not occur to the first stimulus of a sequence. As discussed in the Introduction to experiment 6, initial and change ORs have been dissociated on the basis of ERP components. The N1-P2 complex appears to be related to the initial OR, whereas an additional N2b-P3a complex, depending on the occurrence of a preceding MMN, is thought to be related to the change OR. The present experiment is concerned with the latter ERP components.

The second hypothesis suggests that, if a deviant stimulus follows a number of presentations of another stimulus, an MMN and P3a will be elicited.

The third hypothesis suggests that, if a deviant stimulus follows the presentation of the same deviant stimulus, a smaller MMN and P3a will be produced than if it was preceded by a different stimulus. This will occur because a neuronal trace of the deviant stimulus will still be present in sensory memory on presentation of the next deviant stimulus. The neuronal trace of the frequent stimulus will also still be present in sensory memory on this trial and so, although the deviant stimulus will match with the trace of the deviant stimulus, it will mismatch with the trace of the frequent stimulus. An overall mismatch will occur but this will be smaller than in the case where the deviant stimulus does not match any of the sensory memory traces.

If subjects are presented with a sequence of frequently occurring stimuli randomly interspersed with occasionally occurring deviant sounds and targets as in the oddball task, Naatanen's model (1990) proposes that, as for the deviant sounds, a mismatch will occur between the target and the trace formed in sensory memory of the frequent stimulus. As the targets are task relevant and require some form of response (e.g. counting, making a button press), the model proposes that their occurrence will elicit a P3b in addition to a P3a. The P3b component may overlap the P3a producing a parietally distributed P3b in the resulting waveform. According to Naatanen (1990) the detection of a target in a one channel attentional task, such as the oddball task, occurs through the 'internal monitoring' for the possible occurrence of the mismatch process which is achieved by a temporary link between the limited capacity system and the mechanisms generating the MMN. So the preattentional discrimination of the stimulus deviation is thought to be carried out by the processing reflected by the MMN but the attentional discrimination of the stimulus, including the determination that it is a target, is carried out by the central executive mechanisms. After the target has been detected as such, the appropriate behavioural response is released and the P3b is elicited. Although Naatanen's theory does not make any prediction concerning a relationship between the magnitude of the MMN and that of the P3b, it would predict that a P3b would only occur in a one channel oddball task if a mismatch had been detected.

A study reported by Squires et al. (1976) showed that the nature of the preceding stimuli affected the amplitude of the P3b elicited by the target stimuli. The size of the P3b elicited by the stimulus A increased with the number of preceding B stimuli and decreased with the number of preceding A stimuli. Squires et al. (1976) proposed that the "event expectancy" affected the amplitude of the P3b. They

suggested that the expectancy was determined by the frequency with which the stimulus occurred within a certain number of stimuli in the sequence. The more frequently the event occurred in that part of the sequence, the greater the expectancy that it would occur again. It was argued that the P3b was larger when expectation was disconfirmed, that is the subject expected the frequent stimulus to occur but a rare target stimulus occurred instead. This study, however, was problematic in that sequential and temporal probability were confounded. If a stimulus occurred frequently within a number of stimuli it also occurred frequently within a period of time.

The effects of temporal and sequential probability on P3b amplitude have been unconfounded by a number of more recent studies. Fitzgerald and Picton (1981) report a study in which manipulation of the interval between stimuli (therefore affecting the temporal probability), whilst maintaining the same stimulus sequence, was found to produce changes in the P3b. The sequential probability of the target stimulus was maintained at 0.20. Five different ISIs were used of 250 ms, 500 ms, 1 s, 2 s, 4s which produced temporal probabilities of 1/1.25 s, 1/2.5 s, 1/5 s, 1/10 s and 1/20 s respectively. Fitzgerald and Picton also showed that simultaneous manipulation of both temporal and sequential probability indicated that temporal probability determined the amplitude of the P3b. Four conditions were used in this experiment. In condition 1 the sequential probability of the targets was 0.1 and the ISI 250 ms giving a temporal probability of 1/2.5 s. In condition 2 the sequential probability of the targets was 0.1 but the ISI was 750 ms giving a temporal probability of 1/7.5 s. In condition 3 the sequential probability of the targets was 0.3 and the ISI 750 ms giving a temporal probability of 1/2.5 s. In condition 4 the sequential probability of the targets was 0.3 and the ISI 2250 ms giving a temporal probability of 1/7.5 s. The amplitude of the P3b was found to increase as temporal

probability decreased. No change in P3b amplitude was found with changes in sequential probability and no interaction was found between temporal and sequential probability. In the study reported by Scott et al. (1989), subjects were presented with a sequence in which the frequent stimuli had been omitted so that only the targets were presented but at the same temporal probability as in sequences in which the frequents were presented. A P3b was elicited which did not differ from that elicited when the frequents were present in the stimulus sequence. Experiment 4, reported in chapter 7, was of a very similar design to the Scott et al., study and produced very similar results with respect to the P3b elicited by the targets. The results of these studies therefore suggest that temporal probability rather than sequential probability is the determinant of P3b amplitude.

In the task in which the frequent stimuli were omitted (Scott et al.,1989; experiments 4a and 4b reported in chapter 7 of this thesis), the long ISIs between stimuli meant that a trace was not present in sensory memory for a long enough period of time for the next stimulus to be compared with it. Despite the impossibility of a mismatch occurring in these tasks, a P3b was elicited by the target tones. The proposal that the targets in an oddball task are detected through the monitoring for a mismatch between the neuronal trace held in sensory memory and features of the presented stimulus is not supported by the results of these tasks. It is possible, however, that different strategies may be employed for the detection of targets in different tasks and that, as the P3b reflects a process which becomes active after the target has been detected through attentional processing, it may be possible to access attentional processing through several different routes, the monitoring for a mismatch being just one such route.

In the present experiment the effect of the local stimulus sequence on the amplitude of the P3a was investigated. As in the other experiments reported here, the deviant stimulus was a novel sound. It was proposed that the P3a would be large in response to a novel sound following the presentation of at least five non-novel sounds (5FT-N), smaller if the novel sound was preceded by a novel sound and intervening frequent sound (N-F-N), smaller again when immediately preceded by the same novel sound (N-N) and smallest when immediately preceded by two novel sounds (N-N-N). As no attempt was made in the present experiment to unconfound the effects of sequential and temporal probability on the P3b, it would be predicted that, as in the Squires et al. (1976) study, a smaller P3b would be elicited when a target immediately followed the presentation of a target than when a target had not been recently presented.

A number of studies have reported changes in the amplitude of the P3a elicited by novel stimuli over the first few presentations of the stimulus. Courchesne et al. (1975) reported a decrease in amplitude of the P3a over the first three presentations of a novel visual stimulus and Courchesne (1978) reported a decrease in P3a amplitude elicited by the novel visual stimuli at Fz over the first sixteen presentations, no change at Cz and an increase in P3a amplitude at Pz on the fifth to the eighth presentations compared with earlier presentations. Similar reports have been made in the auditory modality, for example Knight (1984) reported a decrease in amplitude of the P3a elicited by novel sounds over the first five presentations of the stimulus and in the somatosensory modality, for example Yamaguchi and Knight (1991a) reported a decrease in P3a amplitude over the first three presentations of a novel somatosensory stimulus. The amplitude of the P300 deflection elicited by the novel sound was measured at the midline for the first 12 presentations of the novel

sound in the present experiment. It was predicted that there would be a decrease in amplitude over the 12 presentations at Fz and an increase in amplitude at Cz and Pz.

METHOD

Subjects

Sixteen subjects took part in the experiment (mean age 21 yrs, range 19-27 yrs; 9 female). All subjects were paid volunteers.

Design

Four sequences were constructed for the experiment. Each subject was presented with one sequence only. The sequence presented to subjects was alternated so that each sequence was heard by a total of four subjects. All sequences consisted of a total of 600 stimuli and were produced by the random mixing of a frequent high (1000 Hz) tone (P=0.7), a target low (750 Hz) tone (P=0.15) and a novel sound (P=0.15).

Each stimulus sequence was constructed to investigate the effect of 9 conditions. The conditions included a) a novel sound which was preceded by no other stimuli in the sequence b) a novel sound immediately preceded by two novel sounds (N-N-N), c) a novel sound immediately preceded by one novel sound (N-N), d) a novel sound preceded by a novel sound and an intervening frequent tone (N-F-N) and e) a novel sound preceded by at least five non-novel stimuli (5FT-N, where FT refers to frequents and occasional targets). The target stimuli were assigned to conditions

analogous to conditions b) to e) of the novel stimuli (i.e. T-T-T, T-T, T-F-T, 5FN-T, where T refers to the target, F to the frequent and 5FN to at least 5 non-targets including both frequents and novels). Each sequence contained at least 10 trials of each condition. The remaining presentations of target stimuli and novel sounds occurred randomly so that order of presentation of the rare stimuli was unpredictable.

Procedure

Prior to the experimental trials, subjects were presented with a sequence of 29 practice trials consisting of high and low tones. This enabled the subjects to become familiar with the targets to be detected in the experiment. For the experimental trials subjects were presented with one 600 trial sequence in 6 blocks of 100 trials with a 30 s break between each block. Subjects were told that a sequence of stimuli would be presented consisting mainly of a high pitched tone with occasional presentations of a low tone and an environmental noise. Subjects were instructed to press a button whenever the low tone occurred, this response was to be as fast as possible whilst avoiding errors. Subjects were instructed that no response was required for the frequent stimuli or the other sound. Responses were made with the preferred hand. Subjects were told that the sequence of stimuli was quite long and that its presentation would be split in to a number of blocks with a short break between each block.

Filtering

The averaged waveforms were filtered by a symmetrically weighted single-step low-pass digital filter (Ruchkin and Glaser, 1978). The extent of filtering was specified

by the experimenter a cut off of 12.2 Hz was used. Heavier filtering of the waveforms in the present experiment compared with the previous experiments reported here was necessary because fewer trials contributed to the averaged waveforms in each condition and therefore the background EEG activity, producing noise in the ERP waveform, would have been averaged out less in the present experiment than in the other experiments reported here. The heavier filtering of the averaged waveforms removed high frequencies making the ERP more visible.

Single trial Analysis

To make it possible to measure peaks in the single trial data the raw EEG waveforms were initially digitally filtered by the symmetrically weighted single-step filter used for filtering the averaged waveforms. In the present experiment the waveform was filtered with a cut off of 12.2 Hz.

DATA ANALYSIS

Preliminary analysis showed an unexpected result for the condition in which the rare stimulus was immediately preceded by two identical rare stimuli (N-N-N, T-T-T). It had been predicted that the P300 deflection elicited in this condition would be of smaller amplitude than that elicited in the other conditions. The reverse was found. Inspection of the stimulus sequences, however, revealed that every time (apart from on approximately 2 occasions) a stimulus was immediately preceded by an identical stimulus it was also followed by the same stimulus. This means that every time two identical rare stimuli occurred in succession, the subjects could be confident that a third identical stimulus would be presented. The sequences had been set up in this

way to maintain the correct probabilities of the three categories of stimuli in the sequence whilst ensuring that each experimental condition occurred at least 10 times throughout the sequence; the resulting methodological problem had not been foreseen. To overcome the problem it would have been necessary to have a very long stimulus sequence. It was therefore decided to eliminate this condition from the analysis and only investigate the effects of the remaining three conditions (X-X, X-F-X, 5FT-X, where X refers to a rare stimulus), as these conditions were unaffected by the above problem but still allowed an adequate investigation of the hypothesis proposed in the Introduction.

The grand average waveforms for the target tone and novel sound are shown in Figures 10.1a and 10.1b, for the conditions in which the stimulus was preceded by one stimulus identical to itself (T-T, N-N); preceded by a stimulus identical to itself and a frequent stimulus (T-F-T, N-F-N) and preceded by at least five stimuli different to the stimulus of interest (5FN-T, 5FT-N).

The waveform elicited by the frequent stimuli (not shown in figures 10.1a and 10.1b) was averaged over a mean of 318 trials (range 231-409). For the targets the waveform for the T-T condition was averaged over a mean of 10 trials (range 3-13), for the T-F-T condition was averaged over a mean of 8 trials (range 3-10) and for the 5FN-T condition was averaged over a mean of 40 trials (range 21-51). For the novel sound the waveform for the N-N condition was averaged over a mean of 8 trials (range 4-11), for the N-F-N condition was averaged over a mean of 8 trials (range 4-10) and for the 5FT-N condition was averaged over a mean of 37 trials (18-50).

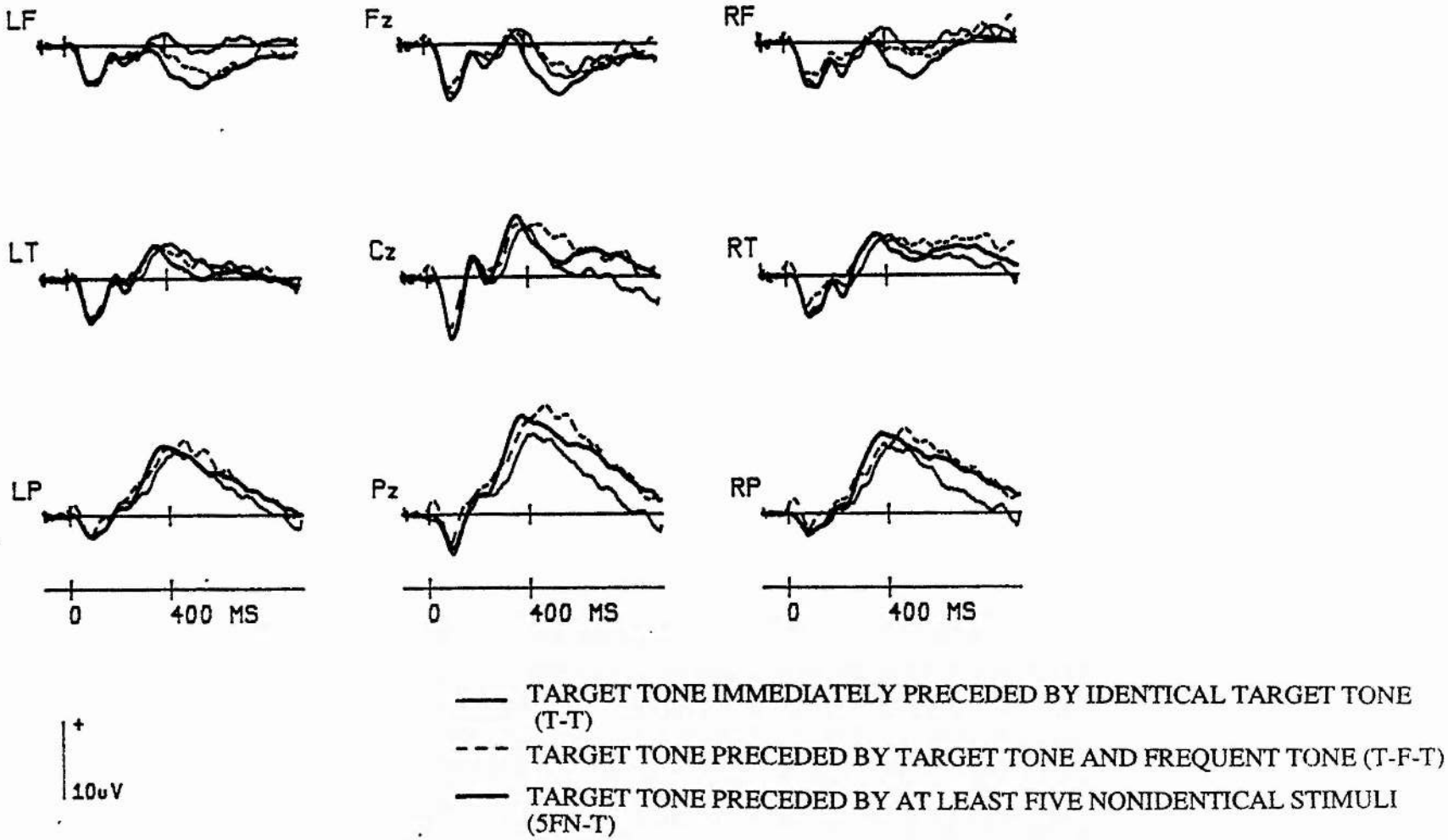


Figure 10.1a Waveforms averaged over 12 subjects for the target tone for the conditions in which the stimulus was preceded by one stimulus identical to itself (T-T); preceded by a stimulus identical to itself and a frequent stimulus (T-F-T); and preceded by at least five stimuli different to the stimulus of interest (5F-T) in experiment 7.

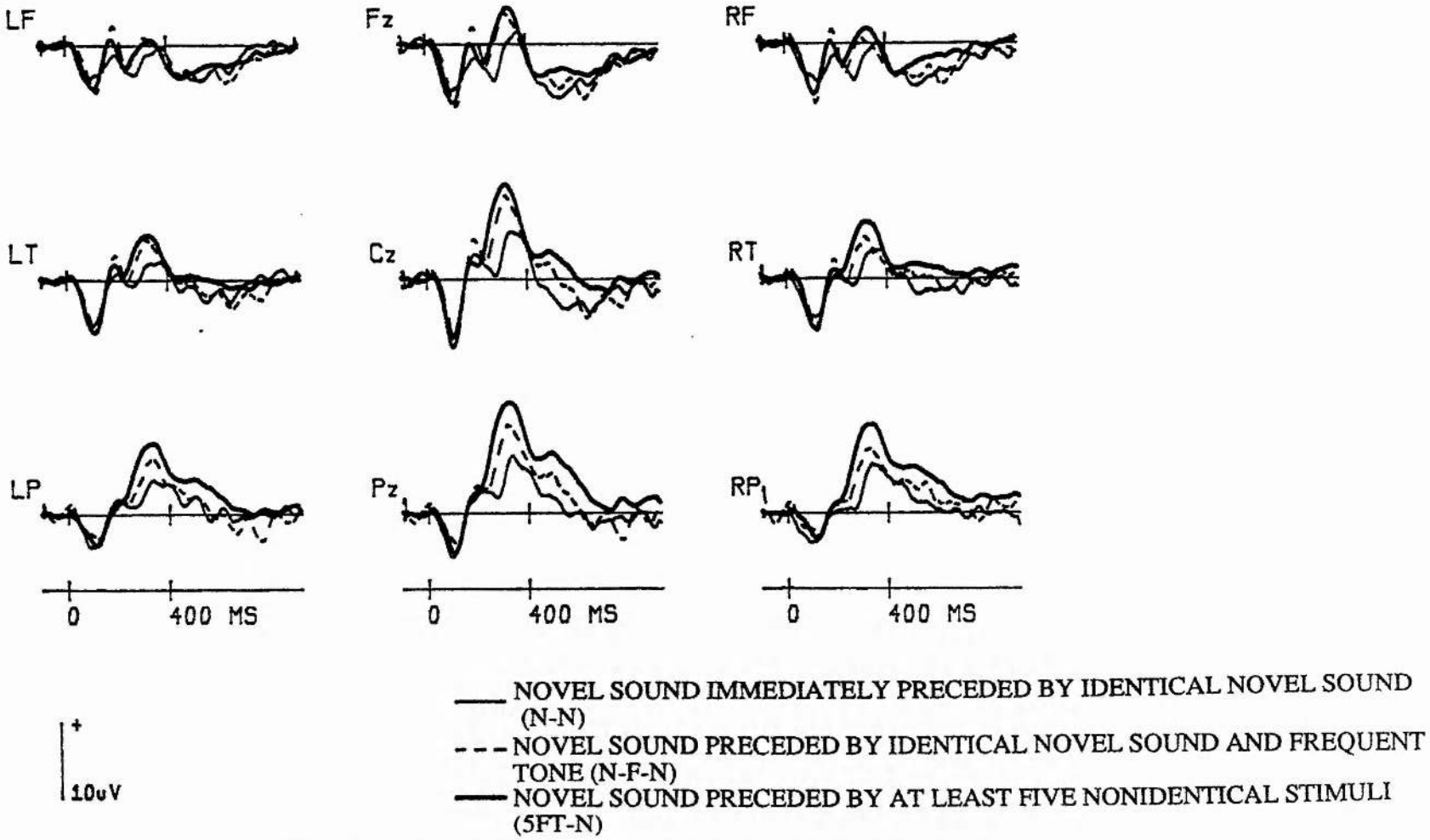


Figure 10.1b Waveforms averaged over 12 subjects for the rare nontarget novel sound for the conditions in which the stimulus was preceded by one stimulus identical to itself (N-N); preceded by a stimulus identical to itself and a frequent stimulus (N-F-N); and preceded by at least five stimuli different to the stimulus of interest (5F-N) in experiment 7.

Peak latencies of the P300, N100 and P170 deflections, as defined in experiment 1, were measured. The peak latency of the P300 deflection in the waveforms elicited by the target tone and rare non-target novel sound was measured at Cz and Pz for each of the four conditions described above. The mean peak latency was found over the two electrode sites. These values were used to investigate latency differences between conditions and to determine latency windows for the analysis of the mean amplitude of the deflection. Separate latency windows were determined for each condition, for each category of rare stimuli, for each subject. The peak latency of the N100 deflection was measured at Cz in the waveforms elicited by the target tone and novel sound in each of the four conditions. As for the P300, separate latency windows were determined for each condition for the two categories of rare stimuli, for each subject. The mean peak latency of the P170 was measured at Fz in the waveforms elicited by the target and rare non-target novel sound for each of the conditions described above. Separate latency windows were determined for each condition for each category of rare stimuli, for each subject. The mean amplitude of the 400-800 ms region was investigated because inspection of the grand averaged waveforms suggested that a frontal negativity and parietal positivity had an onset at approximately 400 ms and continued for approximately 400 ms.

The latency of the P300, N100 and P170 deflections were investigated by 16*2*3 (subject*stimulus*condition) ANOVAs. The mean amplitude in the latency windows determined for the P300, N100 and P170 deflections and the mean amplitude of the 400-800 ms region were investigated by 16*2*3*3*3 (subject*stimulus*condition*chain*site) ANOVAs before and after rescaling. An additional 16*3*3*3 (subject*condition*chain*site) ANOVA was performed on the amplitude of the P300 elicited by the novel sound to investigate further the effect of condition on the P300 elicited by this stimulus. A 16*3*3 (subject*condition*chain)

ANOVA was performed on the amplitude of the novel P300 separately for frontal sites and parietal sites. If local stimulus sequence was having an effect on the anteriorly distributed P3a the largest effect would be expected to be seen at frontal sites and if it has its effect on the posteriorly distributed P3b the largest effect would be expected at parietal sites. Separate analyses at frontal and parietal sites would allow an investigation of whether stimulus sequence (therefore condition, in the present experiment) has an effect on either or both of the components thought to be contributing to the novel P300 deflection. The target P300 was investigated by a 16*3*3 (subject*condition*chain) ANOVA at parietal sites only which is where the P3b, the component thought to be elicited by the targets, is of maximal amplitude and so would be the sites where local stimulus sequence would have a maximal effect if it were affecting the P3b. 16*3*3 (subject*condition*chain) ANOVAs were also performed on the N100 and P170 deflections at frontal sites only. The N100 was investigated at frontal sites because inspection of the grand averaged waveforms suggested a possible refractory effect which was largest at frontal sites. The P170 was investigated at frontal sites because at these sites there is less overlap and contamination of the P170 measurements by the P300 deflection.

Inspection of the waveforms in Figure 10.1a and 10.1b shows a negative deflection following the P170 and preceding the P300 deflection. The negative deflection probably results from overlapping MMN and N2b components. It would be interesting to look at changes in the amplitude of this deflection across the stimulus conditions because the hypotheses concerning changes in P3a amplitude were proposed on the basis of observed changes in the MMN (Sams et al., 1984). As discussed in previous experiments, it is very difficult to obtain a useful measure of the size of the N200 deflection. As the N200 is superimposed on the rising slope of the P300 deflection, it is often above the baseline so prestimulus baseline to peak

amplitude measures only indicate how far above the baseline the peak is, not its amplitude. On some occasions the peak occurs above the baseline whereas in other conditions it occurs below the baseline, this may be due to an overall shift, either positive or negative, of the waveform rather than changes in the N200 region. Peak to peak amplitude measurements could be made but this has the disadvantage of the difficulty in knowing whether an apparent change in amplitude of, for example the N200, is due to a change in its amplitude or a change in amplitude of the peak against which it is being compared, for example P170/P300. Additionally, as the stimuli are being attended in the present experiment, the N200 deflection will consist of both MMN and N2b components. Changes in the N200 could be due to changes in either or both components. Due to these complications and difficulty in measurement, it was decided not to analyse the N200 deflection in the present experiment.

The peak amplitude of the P300 deflection elicited by the novel sound was measured at Fz, Cz and Pz for the second to the twelfth presentation of the novel sound in the first block of trials. Measurements were made from the individual subjects' waveforms. The first presentation of the novel sound was not used because, as this occurred as the first trial of the sequence and subjects were uncertain when the sequence would begin, the waveform tended to be contaminated by eye artifacts, e.g. blinks. A 16*11*3 (subject*trial*site) ANOVA was performed on the amplitude of the P300 elicited by the novel sound.

The reaction times for responses to the target tones were analysed by a 16*3 (subject*condition) ANOVA.

RESULTS

P300 before rescaling

The P300 deflection measured at Cz and Pz was found to have a significantly longer mean peak latency in the waveforms elicited by the target (375.7 ms) than in the waveforms elicited by the novel sound (329.9 ms) ($F(1,15)=46.141$, $P<0.001$). The mean peak latency of the P300 deflection was found to differ significantly between conditions ($F(1.7,24.8)=12.125$, $P<0.001$) but no significant stimulus by condition interaction was found. The effect of condition was investigated by a Newman Keuls test comparing the latency of the P300 deflection across condition, collapsed over stimulus. The P300 deflection elicited in response to the stimulus immediately preceded by an identical stimulus (N-N, T-T) was significantly longer than that elicited by a stimulus preceded by an identical stimulus and an intervening frequent stimulus (N-F-N, T-F-T) and that elicited by a stimulus preceded by at least five nonidentical stimuli (5FT-N, 5FN-T). The trend of the means suggested that the P300 elicited by the stimulus preceded by an identical stimulus and an intervening frequent stimulus was longer than that elicited by the stimulus preceded by at least five different stimuli but Newman Keuls tests showed that this difference was not statistically significant.

The results of the analysis of the amplitude data are shown in Table 10.1. It can be seen that no significant main effects of stimulus or condition were found.

Table 10.1 shows significant main effects of chain and site. A significant chain by site interaction was obtained which interacted significantly with stimulus producing a significant three way interaction between stimulus, chain and site. This interaction

will be discussed in relation to the rescaled data. The significant stimulus by chain interaction was investigated by Newman Keuls tests comparing the difference in amplitude of the P300, elicited by targets and novel sounds, across sites. It was found that the difference in amplitude of the P300 elicited by the two categories of rare stimuli differed between midline and lateral sites. The interaction was obtained because the novel P300 was larger in amplitude than the target P300 at the midline, whereas at lateral sites the target P300 was larger in amplitude than the novel P300. A significant condition by chain interaction was found which will be discussed in relation to the rescaled data.

A significant stimulus by condition effect was obtained. Newman Keuls post hoc tests comparing the amplitude of the P300 across condition for each stimulus showed that for the targets no significant difference was found between conditions. In contrast, the P3a elicited by the novel sounds showed a change in amplitude across conditions which was consistent with the predictions made in the Introduction (see Figure 10.2). The post hoc tests showed that the P300 elicited by the novel sound preceded by at least five non-novel stimuli was significantly larger in amplitude than that elicited by the novel sound when immediately preceded by the same novel stimulus. No significant differences were found between either of these two conditions and the condition in which the novel sound was preceded by the same novel sound and a frequent tone, although, as shown in Figure 10.2, the direction of the change was as predicted.

The ANOVA performed only on the P3a amplitude data showed a significant main effect of condition ($F(1.3,20.2)=8.320$, $P=0.005$). This was investigated further by planned comparisons between the mean P3a amplitudes (collapsed over chain and site) elicited by stimuli in the three conditions. In the Introduction it was predicted

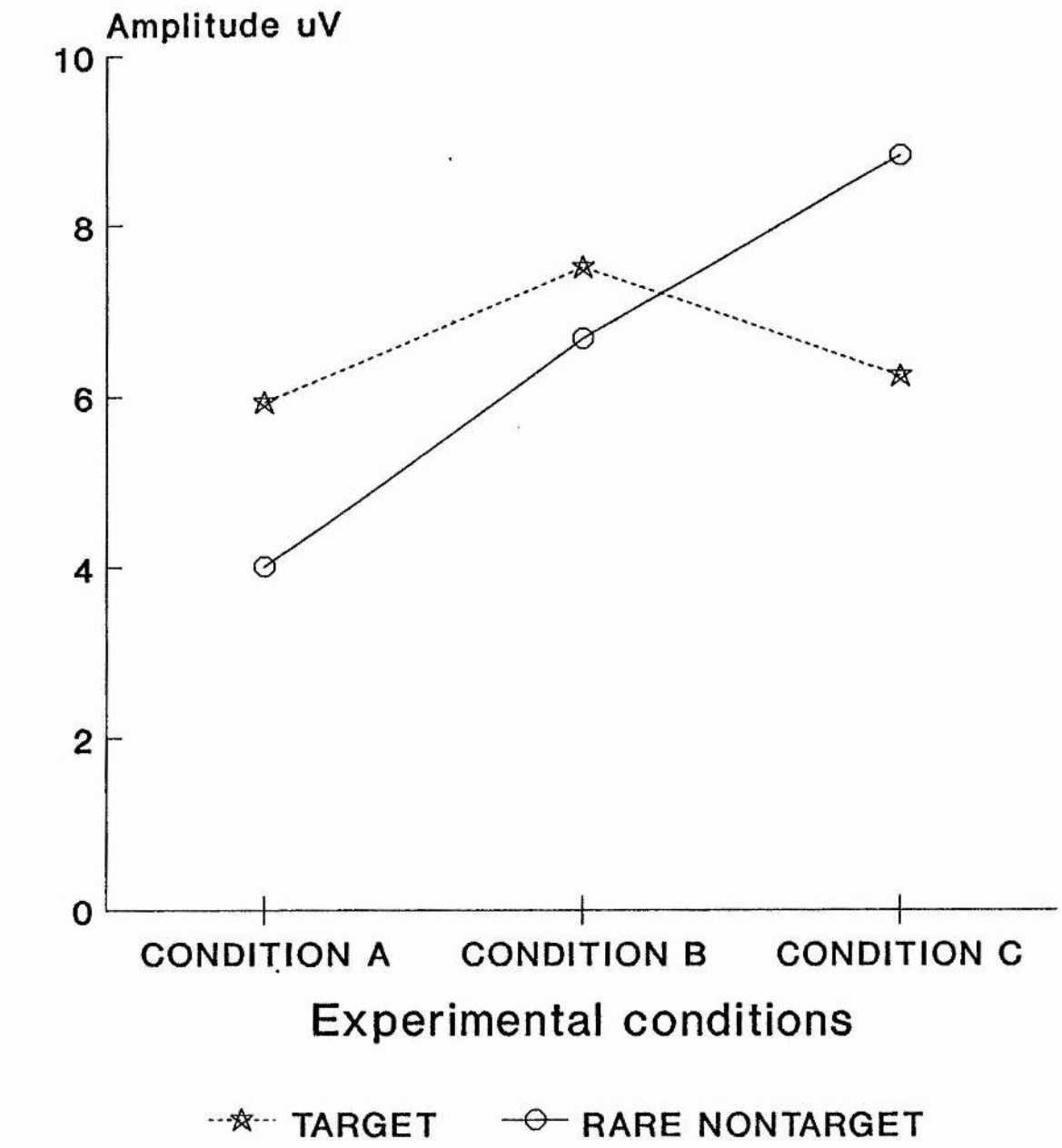
Table 10.1. ANOVA summary table for analysis of the amplitude of the P300 elicited by target and rare non-target stimuli for each of the three experimental conditions, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Stimulus (S)	1,15	0.01	0.940
Condition (CC)	1.3,19.6	3.44	0.070
Chain (CH)	1.8,27.6	40.53	0.000*
Site (ST)	1.2,18.6	94.44	0.000*
S*CC	1.8,27.3	6.41	0.006*
S*CH	1.9,28.9	4.14	0.028*
S*ST	1.2,17.6	3.26	0.084
CC*CH	3.4,50.6	8.34	0.000*
CC*ST	1.9,28.3	4.08	0.030*
CH*ST	2.5,37.1	6.87	0.002*
S*CC*CH	2.8,41.3	1.62	0.203
S*CC*ST	2.2,33.1	0.62	0.560
S*CH*ST	3.1,46.8	5.73	0.002*
CC*CH*ST	5.4,81.1	0.87	0.507
S*CC*CH*ST	5.1,76.3	0.80	0.554

RESCALED AMPLITUDE			
Factors	df	F	Prob
Stimulus (S)	1,15	0.46	0.505
Condition (CC)	1.3,19.1	0.04	0.893
Chain (CH)	1.8,27.5	37.03	0.000*
Site (ST)	1.3,18.8	94.13	0.000*
S*CC	1.6,24.5	0.10	0.869
S*CH	1.9,28.3	4.38	0.024*
S*ST	1.2,17.6	2.19	0.156
CC*CH	3.4,50.3	2.71	0.049*
CC*ST	1.7,25.8	0.86	0.416
CH*ST	2.5,37.3	6.53	0.002*
S*CC*CH	2.5,36.8	0.79	0.485
S*CC*ST	2.2,33.3	0.15	0.883
S*CH*ST	3.1,46.7	5.44	0.002*
CC*CH*ST	4.7,70.2	0.79	0.555
S*CC*CH*ST	4.7,69.8	0.98	0.433

* indicates statistical significance at the 0.05 level or better

Figure 10.2 Graph illustrating the amplitude of the P300 elicited under the three experimental conditions by the target and rare nontarget stimuli in experiment 7.



that the smallest P3a would be elicited by a novel sound immediately preceded by an identical novel sound and the largest P3a elicited by a novel sound when preceded by at least five non-novel sounds with the third condition producing a P300 deflection with an amplitude somewhere between the two. The results of the planned contrasts showed that the P3a elicited by a novel sound immediately preceded by an identical novel sound (N-N) was significantly smaller than that elicited in the other two conditions but the P3a elicited by a novel sound preceded by a novel sound and an intervening frequent (N-F-N) did not differ significantly from that elicited by a novel sound preceded by at least 5 non-novel sounds (5FT-N).

Although the condition by site interaction was not significant ($F(1.9,28.4)=2.225$, $P>0.05$), inspection of the grand averaged waveforms suggests that the change in amplitude between conditions may be occurring more over parietal sites than over frontal sites. If this were the case it would suggest that stimulus sequence may be having an effect on the posteriorly distributed P3b rather than the more anteriorly distributed P3a which together are thought to produce the novel P300 deflection. This was further investigated by performing separate ANOVAs on the amplitude of the novel P300 at frontal and parietal sites. The ANOVA on novel P300 amplitude at frontal sites showed no significant main effect of condition, however, a significant condition by chain interaction was obtained ($F(2.7,40.6)=3.359$, $P<0.05$). Newman Keuls tests showed that the interaction was obtained because the difference in amplitude between the P300 elicited by a novel sound preceded by at least five non-novel sounds (5FT-N) and both a novel sound preceded by a novel sound and intervening frequent (N-F-N) and that immediately preceded by a novel sound (N-N) was larger over right hemisphere and midline sites than over the left hemisphere. The difference in amplitude of the novel P300 between that elicited by a novel

sound preceded by a novel sound and an intervening frequent (N-F-N) and a novel sound immediately preceded by a novel sound (N-N) was larger at the midline than at the right hemisphere but did not differ between the midline and left hemisphere or right and left hemisphere sites.

The ANOVA performed on the amplitude of the novel P300 at parietal sites showed a significant main effect of condition ($F(1.9,29.1)=10.126$, $P=0.001$). Newman Keuls tests showed that the P300 elicited by a novel sound preceded by at least five non-novel sounds (5FT-N) was significantly larger in amplitude than that elicited by a novel sound preceded by a novel sound and intervening frequent sound (N-F-N) and that elicited by a novel sound immediately preceded by a novel sound (N-N), no difference was found between these latter two conditions. A significant condition by chain interaction was obtained ($F(3.3,49.4)=5.325$, $P<0.005$). The interaction was investigated by Newman Keuls tests comparing the differences in novel P300 amplitude between electrode chains for each condition. For the P300 elicited by the novel sound immediately preceded by an identical novel sound (N-N) the difference in amplitude between the midline and left hemisphere was significantly larger than that between the midline and right hemisphere or right and left hemisphere sites which did not differ significantly. The P300 elicited by a novel sound preceded by a novel sound and an intervening frequent tone (N-F-N) had a significantly larger difference between both midline and left and midline and right hemisphere sites than between left and right hemisphere sites. The differences between midline and both right and left lateral sites did not differ significantly. The P300 elicited by a novel sound preceded by at least five non-novel sounds (5FT-N) had a significantly larger difference between the midline and left and the midline and right hemisphere than the difference between right and left hemispheres. The difference in amplitude

between midline and left hemisphere was significantly larger than that between the midline and right hemispheres.

An ANOVA was performed on the amplitude of the target P300 (thought to be reflecting the contribution to the waveform of the P3b component) at parietal sites only. The results of the ANOVA showed no significant effect of condition ($F(1.4,21.7)=1.441$) and no significant condition by chain interaction ($F(3.0,44.5)=1.396$).

P300 after rescaling

As shown in Table 10.1, significant main effects of chain and site were obtained. A significant chain by site interaction was obtained which interacted significantly with stimulus. As shown in Figures 10.3a and 10.3b, the P300 elicited by the target had a parietal maximum over all three electrode chains, whereas that elicited by the novel sound was distributed more over central sites than that elicited by the target at the midline but had a parietal maximum at lateral sites. The three way interaction between stimulus, chain and site was investigated by Newman Keuls tests comparing the difference in rescaled amplitude between the two conditions, across site, for each electrode chain. It was found that, at the midline, the difference between stimuli was significantly larger at vertex than at parietal sites but did not differ between frontal and vertex or frontal and parietal sites. This was because, as suggested by Figures 10.3a and 10.3b, the P300 deflection elicited by the novel sound was distributed more over the vertex than the target but did not differ in distribution at parietal and frontal sites. At lateral sites the difference between the two conditions did not differ significantly between the three electrode sites.

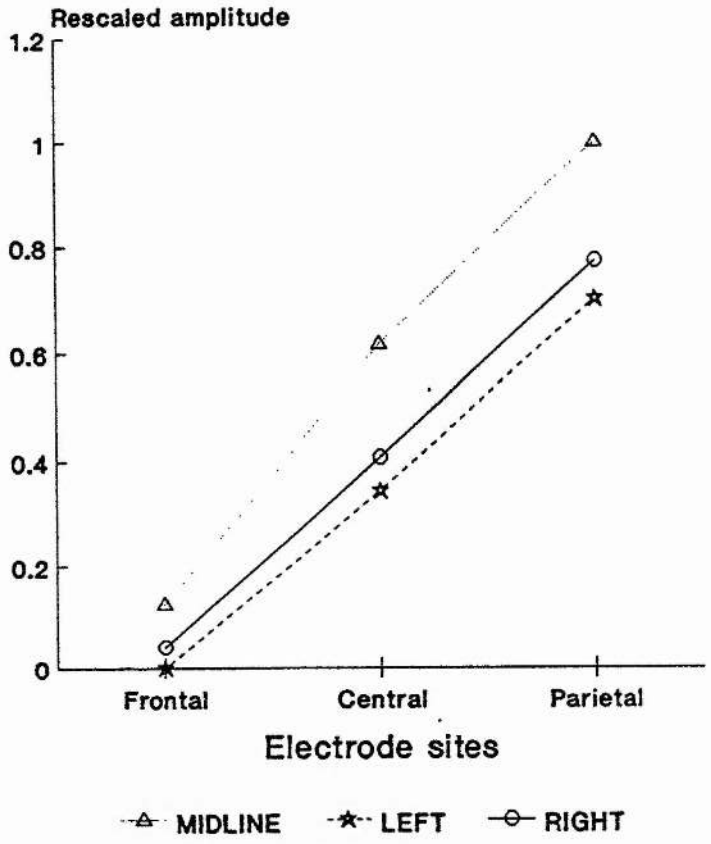


Figure 10.3a Graph illustrating the distribution of rescaled amplitude of the target P300 deflection across site for each electrode chain in experiment 7.

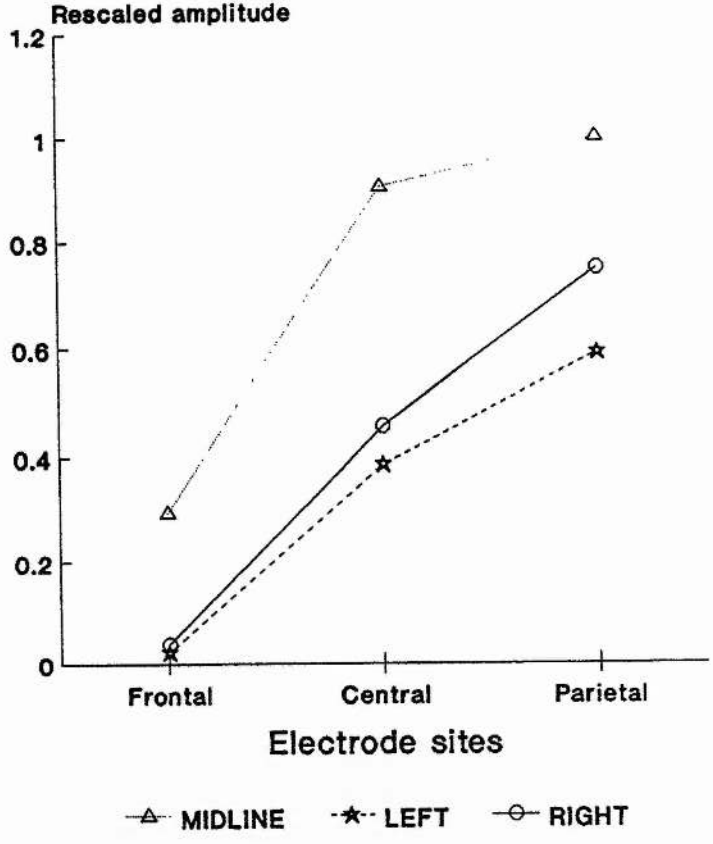


Figure 10.3b Graph illustrating the distribution of rescaled amplitude of the rare nontarget P300 deflection across site for each electrode chain in experiment 7.

Figure 10.4 Graph illustrating the distribution of the P300 deflection over electrode chains for each condition in experiment 7 (collapsed over stimulus and site).

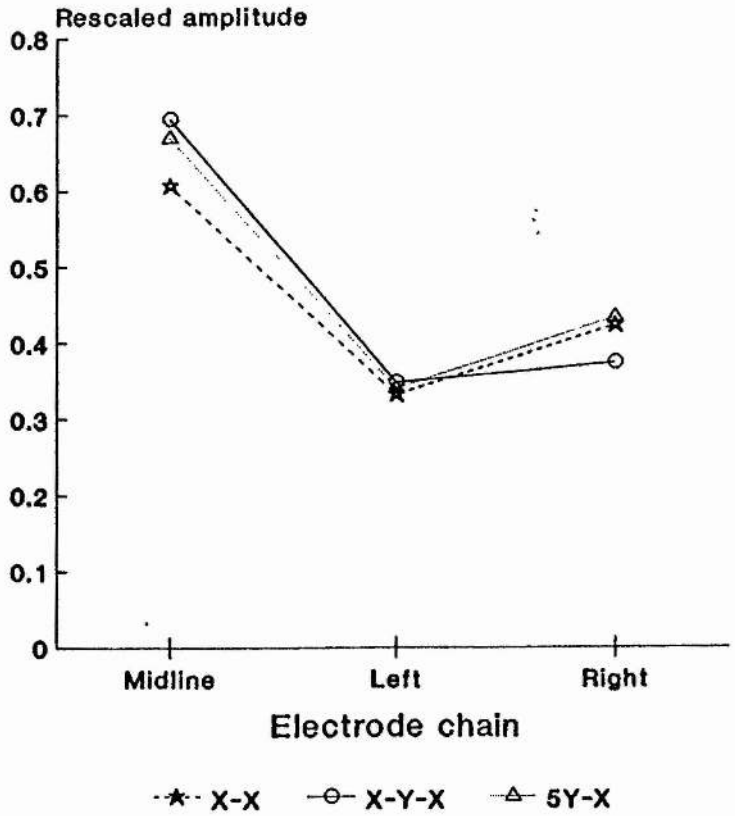


Table 10.1 shows a significant stimulus by chain interaction. Newman Keuls tests were performed comparing the difference in P300 rescaled amplitude between targets and novel sounds, across chain. The interaction occurred because there was a significantly larger difference between target and novel P300 rescaled amplitude at the midline than at lateral sites which did not differ. The novel P300 was distributed significantly more over the midline than the target P300.

As shown in Table 10.1, a significant interaction was obtained between condition and chain. The differences between conditions in the rescaled amplitude of the P300, collapsed over stimulus, were compared across electrode chain using Newman Keuls tests. No significant differences across chain were found between the P300 deflections elicited by stimuli which were preceded by at least five different stimuli or for the deflections elicited by the stimuli immediately preceded by an identical stimulus. The P300 elicited by a stimulus which was preceded by the identical stimulus and a frequent stimulus was distributed more over the midline and less over right hemisphere sites than that elicited in the other two conditions (see Figure 10.4). No significant three way interaction with stimulus was obtained.

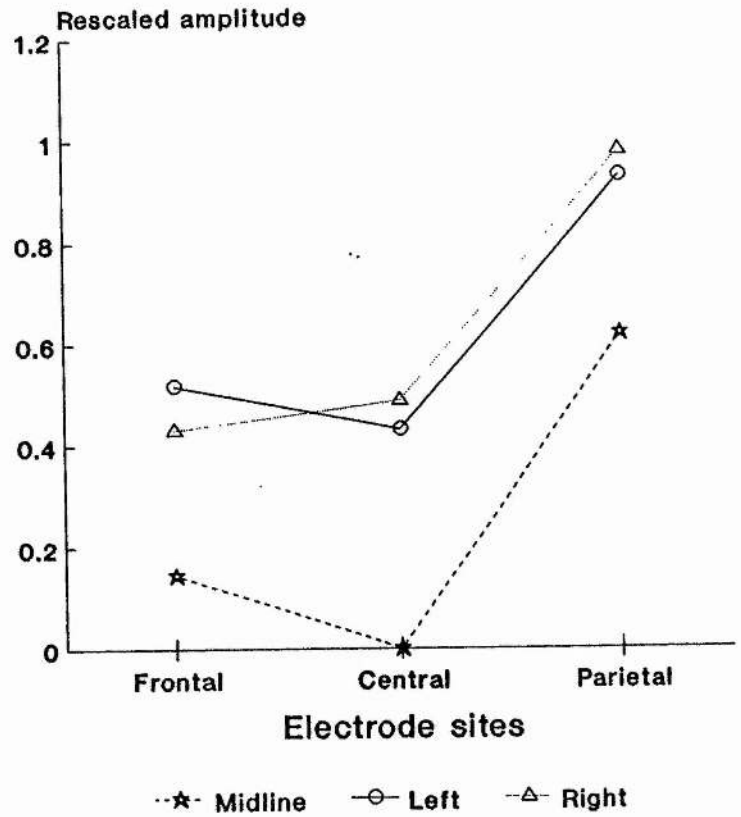
N100 before rescaling

The mean peak latency of the N100 was found to be 103.8 ms in response to the target tone and 107.7 ms in response to the novel sound. The difference in N100 peak latency between the two stimuli was not statistically significant. No significant difference in latency was found between the three conditions and no significant stimulus by condition interaction was obtained.

The results of the analysis of the amplitude data are shown in Table 10.2 of the Appendix. There was no significant main effect of stimulus or condition. The ANOVA performed at frontal sites only for both the targets and the novel sounds showed no significant effect of stimulus or condition and no significant interactions with either stimulus or condition (see Table 10.2 of Appendix). An additional ANOVA was performed on the amplitude of the N100 elicited by the novel sounds at frontal sites only. This analysis was performed because inspection of the waveforms suggested that there may be a refractory effect on the N100 elicited by the novel sounds which is not present in the waveforms elicited by the targets. The results of the ANOVA showed no significant main effect of condition ($F(1.7,25.7)=0.151$) but a significant condition by chain interaction was obtained ($F(2.7,40.2)=3.353$, $P<0.05$). Newman Keuls tests comparing the amplitude of the novel N100 across electrode chain for each condition, showed that the N100 elicited by a novel sound immediately preceded by at least five non-novel sounds (5FT-N) and that elicited by a novel sound immediately preceded by a novel sound (N-N) was significantly more negative at the midline than at lateral sites. The N100 elicited by a novel sound and an intervening frequent tone (N-F-N) was significantly more negative over right hemisphere and midline sites than over left hemisphere sites.

Table 10.2 shows significant main effects of chain and site and a significant chain by site interaction which will be discussed in relation to the rescaled data. No other interactions were significant.

Figure 10.5 Graph illustrating the distribution of the N100 across site for each electrode chain in experiment 7 (collapsed over stimulus and condition).



N100 after rescaling

Table 10.2 of the Appendix, shows significant main effects of chain and site. A significant chain by site interaction was obtained. As shown in Figure 10.5, the N100 was more negative at frontal and central sites than at parietal sites for all electrode chains. The interaction was investigated by Newman Keuls tests comparing the difference in N100 amplitude between sites, across chain. The difference in N100 between central and parietal sites was larger at midline than at lateral sites which did not differ. The difference between central and frontal sites did not differ between midline and left hemisphere sites both showing a slight increase in N100 amplitude from frontal to central sites, however, the change over the right hemisphere was significantly different from that over the other two chains, showing a slight decrease in N100 amplitude from frontal to central sites.

P170 before rescaling

The P170 was found to have a mean peak latency of 191.5 ms in response to the targets and 188.5 ms in response to the novel sound. This difference in latency was not statistically significant. No significant main effect of condition or stimulus by condition interaction was obtained.

The results of the analysis of the amplitude data are shown in Table 10.3 of the Appendix. It can be seen that significant main effects of chain and site were obtained. A significant interaction was found between chain and site. Newman Keuls tests comparing the amplitude of the P170 across site for each chain showed that at the midline the P170 did not differ significantly in amplitude between central and parietal sites but was significantly larger at these sites than at frontal sites.

Laterally no significant differences were found between site. Newman Keuls tests comparing P170 amplitude across chain, for each site, showed no significant difference in amplitude between chains at frontal sites but at central and parietal sites the P170 was found to be significantly larger at midline than at lateral sites which did not differ.

Table 10.3 of the Appendix, shows a significant condition by site interaction. Newman Keuls tests showed that the P170 elicited by rare stimuli immediately preceded by an identical stimulus had a larger amplitude at central and parietal sites than at frontal sites whereas the P170 elicited by stimuli in the other two conditions showed no significant difference in amplitude across site.

The ANOVA performed at frontal sites on the P170 elicited by the novel sounds and the target tones showed no significant main effect of stimulus or condition and no significant interactions with condition (see Table 10.3 of appendix). A separate analysis was performed at frontal sites for the novel P170 because in the grand averaged waveforms of the present experiment the novel P170 appeared to show a difference in amplitude between conditions which was not present in the waveforms elicited by the targets. No significant effect of condition was found ($F(2.0,29.5)=2.782$).

<u>P170 after rescaling</u>

Table 10.3 of the Appendix shows significant main effects of chain and site. A significant interaction was found between chain and site which interacted significantly with stimulus. This three way interaction was obtained because the P170 produced in response to the targets had a centro-parietal maximum at midline

sites but a parietal maximum at lateral sites, whereas that elicited by the novels had a central maximum for all electrode chains. No other interactions were found to be significant.

400-800 ms region

400-800 ms region elicited by targets at all electrode sites

The results of the ANOVA are shown in Table 10.4 of the Appendix. It can be seen that no significant main effect of condition was found. Significant main effects of chain and site were obtained. A significant condition by chain interaction was found. Newman Keuls tests comparing the amplitude of the 400-800 ms region across chain for each condition showed that for the condition in which a target was immediately preceded by an identical target, and the condition in which the target was immediately preceded by at least five non-targets, no difference in amplitude was found between chains. When a target was immediately preceded by a target and intervening frequent, the 400-800 ms region was more positive over midline and right hemisphere than left hemisphere sites. Newman Keuls tests investigating differences between chains across conditions showed that the difference in amplitude between midline and right and right and left hemisphere sites did not differ significantly between conditions. The difference in amplitude between midline and left hemisphere sites was significantly larger when elicited by a target preceded by at least five non-targets and by a target preceded by a target and intervening frequent than by a target immediately preceded by an identical target. No significant difference was found between the former two conditions.

A significant condition by site interaction was obtained. Newman Keuls tests comparing the difference in amplitude between sites across condition showed that the differences between parietal and central, parietal and frontal and central and frontal sites were larger in the two conditions in which the target was not preceded by an identical stimulus than when it was. In other words there was a steeper increase in positivity from frontal to parietal sites for the two conditions in which the target was immediately preceded by a non-target than in the condition in which it was immediately preceded by a target.

A significant chain by site interaction was obtained which was investigated by comparing the differences between sites across chain. The differences between all sites were larger at the midline than laterally. The increase in positivity from frontal to parietal sites was larger at the midline than at lateral sites.

Inspection of the waveforms and the effects of site found in the present analysis suggest that this region of the waveform consists of a negative deflection at frontal sites and a posterior positive deflection. The grand averaged waveforms suggest that these deflections are being modulated differently in the different conditions. Therefore the 400-800 ms region was investigated by performing separate ANOVAs on the 400-800 ms region at frontal and posterior electrode sites.

400-800 ms region elicited by targets at frontal sites

The results of the analysis are shown in Table 10.5 of the Appendix. No significant main effect of condition was found but a significant condition by chain interaction was obtained. The interaction was investigated by comparing the 400-800 ms region across chain for each condition. The 400-800 ms region elicited by a target

immediately preceded by an identical target was less negative at frontal lateral sites than at Fz but did not differ significantly between lateral sites. The 400-800 ms region elicited by a target immediately preceded by a target and intervening frequent and that elicited by a target preceded by at least five non-targets was less negative over the right frontal sites than over Fz and left frontal but no significant amplitude difference was found between left frontal sites and Fz.

400-800 ms region elicited by targets at parietal sites

The results of the analysis are shown in Table 10.5 of the Appendix. A significant main effect of condition was obtained which interacted significantly with chain. The condition effect was obtained because the 400-800 ms region of the waveform elicited by a target preceded by a target and intervening frequent, and a target preceded by at least five non-targets, was significantly larger than that elicited by a target immediately preceded by a target. The interaction was investigated by comparing the amplitude of the 400-800 ms region across chain for each condition. A target immediately preceded by an identical target elicited a 400-800 ms region which did not differ significantly in amplitude across electrode chains. A target preceded by a target and a frequent stimulus elicited a 400-800 ms region which was larger at the midline than at lateral sites which did not differ. When the target was preceded by at least five non-targets the 400-800 ms region was larger in amplitude over the midline than left hemisphere but did not differ significantly between midline and right or left and right hemisphere sites.

400-800 ms region elicited by novel sound at all sites

The results of the ANOVA are shown in Table 10.6 of the Appendix. It can be seen that no significant effect of condition and no significant interactions with condition were obtained. No significant main effect of chain was found but a significant main effect of site was obtained which interacted significantly with chain. Newman Keuls tests comparing the difference in amplitude between sites across chain showed that the difference in amplitude between parietal and central sites was larger at the midline than at left hemisphere sites but did not differ in amplitude between midline and right hemisphere sites and right and left hemisphere sites. The difference in amplitude between both parietal and frontal sites and central and frontal sites was significantly larger at the midline and right hemisphere sites than at left hemisphere sites but did not differ between the midline and right hemisphere.

400-800 ms region elicited by novel sound at frontal sites

The results of the ANOVA are shown in Table 10.7 of the Appendix. No significant main effect of condition or interaction with condition was obtained. The significant main effect of chain showed that the 400-800 ms region was significantly more negative at the midline than at lateral sites which did not differ.

400-800 ms region elicited by novel sound at parietal sites

Results of the analysis are shown in Table 10.7 of the Appendix. The significant main effect of condition was obtained because the 400-800 ms region was significantly more positive in the waveforms elicited by a novel sound preceded by at least five non-novel stimuli than in the waveforms elicited by a novel sound

which was immediately preceded by an identical stimulus and the waveforms elicited by a novel sound preceded by a novel sound and intervening frequent. No significant difference in amplitude was found between the 400-800 ms region of the waveforms elicited by a novel sound immediately preceded by a novel sound and intervening frequent or a novel sound immediately preceded by an identical novel sound.

A significant main effect of chain was obtained. Newman Keuls tests showed that the 400-800 ms region did not differ significantly in amplitude between right lateral and midline sites but was significantly more positive at both than over left lateral sites. No significant condition by chain interaction was obtained.

Single trial analysis of the novel P300 deflection

The results of the ANOVA performed on the amplitude of the P3a elicited from the second to the twelfth presentation of the novel sound showed no significant main effect of trial ($F(5.8,86.8)=1.768$). A significant main effect of site was obtained ($F(1.4,21.4)=69.413$, $P<0.001$). Newman Keuls tests comparing the amplitude of the P3a across site, collapsed over trials, showed that the amplitude of the P3a did not differ between central and parietal sites but was significantly larger at these sites than at frontal sites. A significant trial by site interaction was obtained ($F(6.8,101.4)=2.579$, $P<0.05$). The mean amplitude of the P3a on each presentation of a novel sound is plotted for each site in the graph of Figure 10.6. The interaction was investigated by comparing the difference in amplitude of the P3a between sites across trials. The difference in P3a amplitude between Fz and Pz was found to be significantly larger on trials 6 and 11 than on trials 8 and 4, significantly larger on

trial 10 than on trials 8, 4 and 5 and significantly larger on trials 9 and 12 than on trials 8, 4, 5, 2 and 7. The difference in amplitude between Fz and Cz was found to be significantly larger on trial 6 than on trial 8, significantly larger on trials 10 and 11 than on trials 8 and 4, significantly larger on trial 12 than on trials 8, 4, 2 and 7 and significantly larger on trial 9 than on trials 8, 4, 2, 7 and 5. The difference in P3a amplitude between Cz and Pz did not differ significantly across sites. As shown in the graph of Figure 10.6, this pattern of differences, indicated by the post hoc tests, was found because the P3a elicited at Cz and Pz was larger in amplitude from trial 9 to trial 12 compared with the preceding trials, whereas that elicited at Fz did not show this change in amplitude.

The results of the ANOVA on the P3a measured in the 11 trials at the three midline electrode sites therefore suggested that there was a step-like increase in amplitude from trial 8 to trial 9 at central and parietal sites but not at frontal sites. This was further investigated by individual ANOVAs investigating changes in amplitude across trials separately for each electrode site. The ANOVA at frontal sites showed no significant effect of trial ($F(6.0,90.5)=0.981$). At central sites a significant effect of trial was found ($F(5.3,79.5)=2.458$, $P<0.05$). Newman Keuls tests showed that the P3a was significantly larger on trials 9 and 11 than on trial 8. A significant effect of trial was also found in the analysis of the P3a at Pz ($F(5.5,83.0)=2.326$, $P<0.05$). Newman Keuls tests showed the P3a to be significantly larger on trial 9 than on trial 8. An ANOVA was performed investigating the difference in amplitude of the P3a across trials at Cz and Pz. No significant trial by site interaction was obtained ($F(4.4,66.2)=0.337$).

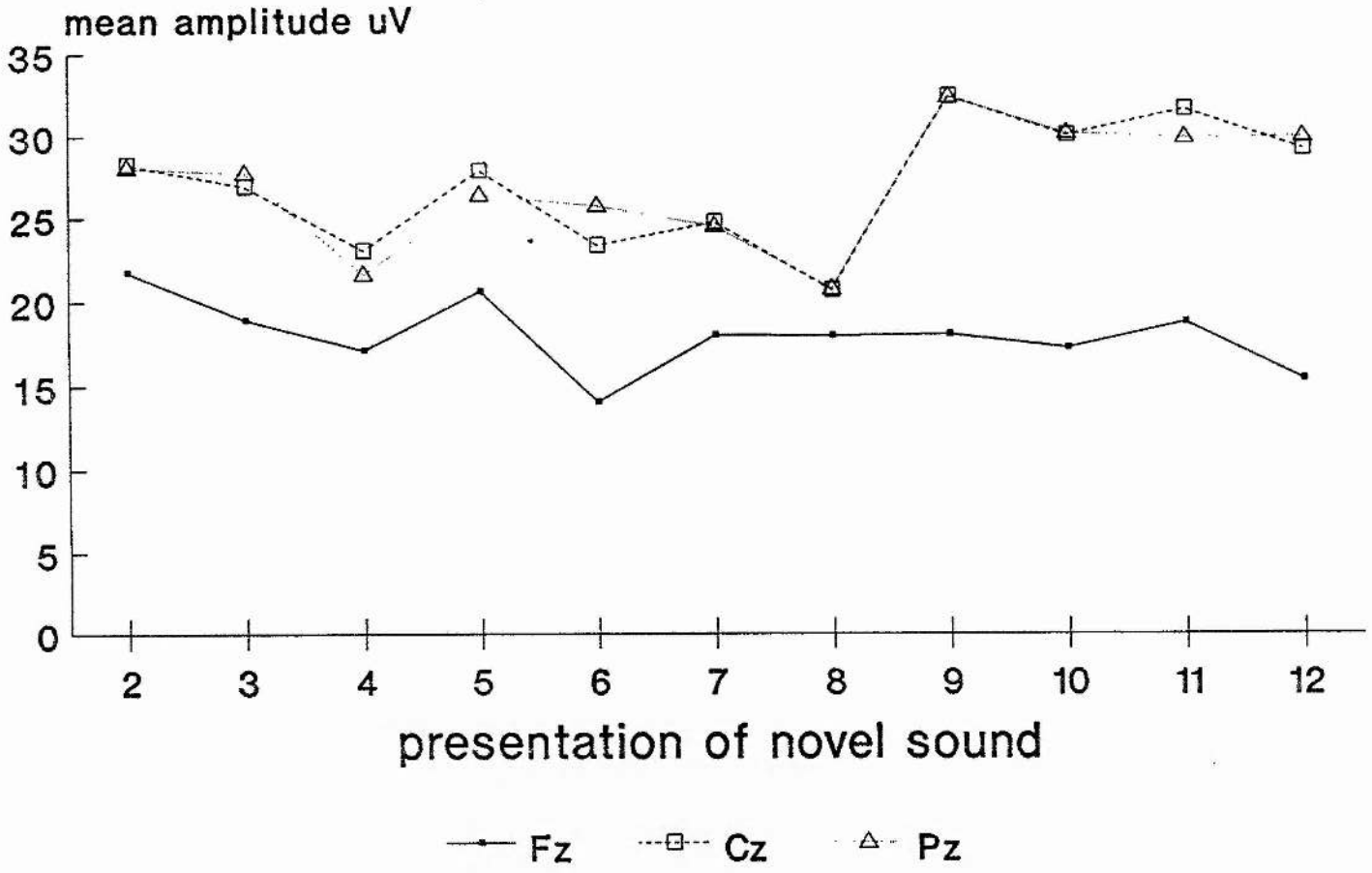


Figure 10.6 Graph illustrating the mean amplitude of the P3a from the second to the twelth presentation of the novel sound at each site in experiment 7.

Table 10.8. Mean reaction time for the response to the target stimulus for each of the three experimental conditions investigated in the ERP analysis and the total number of hits and false alarms made during the presentation of the 600 trial sequence of experiment 7.

	MEAN	SD
REACTION TIME (ms)		
CONDITION		
T-T	508.8	113.3
T-F-T	526.2	118.0
5FN-T	513.9	110.8
TOTAL HITS	88.9	1.4
TOTAL FALSE ALARMS	3.0	2.2

Behavioural data

The mean reaction times to respond to the target tones for the conditions in which:

i) the target was immediately preceded by one target

ii) the target was preceded by a target and a frequent tone

iii) the target was preceded by at least five non-targets

are shown in Table 10.8. The total number of correctly detected targets and the total number of false alarms made during the presentation of the sequence are also shown in Table 10.8. The ANOVA comparing the mean reaction time over the three conditions showed no significant effect of condition ($F(1.7,25.0)=0.497$).

Summary of results

As in Experiment 1, the target tones elicited a P300 deflection with a parietal maximum over all electrode chains (P3b). The amplitude of this deflection did not differ between electrode chains. The novel sounds elicited a P300 deflection with a more anterior distribution than that elicited by the tones at midline sites but with a parietal maximal distribution at lateral sites (P3a). The P3a was larger in amplitude at midline than lateral sites. The P3b elicited by the target tones had a longer latency than the P3a elicited by the novel sounds. For both categories of rare stimuli, the latency of the P300 deflection elicited by a stimulus immediately preceded by an identical stimulus was significantly longer than that obtained when the stimulus was preceded by one or more different stimuli. The P300 deflection elicited by the novel stimuli was larger in amplitude than that elicited by the target tones at the midline with the reverse being true at lateral sites. The P3b elicited by the targets did not differ significantly in amplitude between conditions, in contrast the P3a was larger in amplitude when the novel sound was preceded by at least 5

stimuli which were not novel sounds than when it was preceded by the identical stimulus, the third condition elicited a P3a with an amplitude midway between the two. This change in amplitude was not restricted to frontal sites. A centro-frontally distributed N100 was elicited by both targets and novel sounds. The N100 showed no significant difference in amplitude between conditions. At frontal sites, where the influence of the P300 is minimal, the P170 elicited by both the targets and novel sounds was also found not to differ significantly in amplitude between conditions. The 400-800 ms region of the waveforms elicited by both novel sounds and target tones did not differ significantly in amplitude between conditions at frontal sites. At parietal sites the 400-800 ms region elicited by a novel sound immediately preceded by a novel sound, and a novel sound preceded by a novel sound and intervening frequent tone, was significantly less positive than that elicited by a novel sound preceded by at least five non-novel sounds. For the targets, the 400-800 ms region was more positive in the two conditions in which the target was preceded by a frequent stimulus than in the condition in which the target was immediately preceded by a target.

DISCUSSION

P300

As reported in experiment 1 and experiment 6, the latency of the target P300 was significantly longer than that of the novel P300. This is consistent with previous reports of the P300 deflection elicited by the target reflecting the contribution to the waveform of a P3b component and that elicited by the novel sound reflecting the contribution of an earlier P3a component. An alternative interpretation mentioned in

the previous experiments was that this latency difference reflected a difference in the ease with which the stimuli could be discriminated. Local stimulus sequence affected the latency of the P300 deflection elicited by both the target tones and the novel sounds. The latency of the P300 deflection was significantly longer if the rare stimulus was immediately preceded by the identical stimulus than if it was preceded by several frequent stimuli. No significant difference in reaction time to respond to the target tone was found between the three conditions. The reaction time results are consistent with the study of Remington (1969) who found that a single repetition of a target in the stimulus sequence was not sufficient to speed up reaction time. In the Remington (1969) study facilitation of reaction time required two or more repetitions of the target. The results of the analysis of the reaction times suggest that there was no difference between the three conditions in the time required to discriminate the targets in order to make a response. Reaction time and P300 latency have been found to be differentially affected by experimental manipulations in a number of studies (see Chapter 1). Kutas et al. (1977) showed that when subjects were to respond as fast as possible, so that reaction time was determined by response selection, the correlation between reaction time and P300 latency was low. In the present experiment, although subjects are instructed to respond accurately, the promptness of their response was emphasised. The reaction time responses may therefore be determined more by response selection than by stimulus evaluation in the present experiment. The conditions used in the present experiment may have had differential effects on response selection and stimulus evaluation. Stimulus evaluation may have taken longer when a rare stimulus was immediately preceded by the same rare stimulus.

A number of the results of the analysis of the P300 amplitude data suggest that, although the averaged waveforms were obtained by averaging together a smaller

number of trials than in the previous experiments, the P300 deflections elicited by the targets and novel sounds appear to be reflecting the same components as in experiments 1 and 6. The target P300 was found to have a parietal maximum over all electrode chains and was distributed equally over the three chains of electrodes. The target P300 was therefore considered to be the P3b. The novel P300 had a more anterior maximum than the target P300 at the midline but a parietal maximum at lateral sites. The novel P300 was larger in amplitude than the target P300 at all electrode chains and, in contrast to the target P300, had a midline maximum. As in experiments 1 and 6, the novel P300 was labelled the P3a. These amplitude and distribution differences in P300 between the two categories of rare stimuli were found for all three conditions. The significant stimulus by condition effect showed that the amplitude of the target P300 and novel P300 changed in a different way over the three conditions.

The amplitude of the target P3b was found not to differ significantly across conditions even when the analysis was only performed at parietal sites where the P3b was of maximal amplitude and any effect on the P3b would be expected to have its maximal effect. This suggests that the local stimulus sequence had little effect on the amplitude of the P3b which is inconsistent with the report of Squires et al. (1976). The study of Fitzgerald and Picton (1981) showed that decreasing temporal probability increased the amplitude of the P3b. The study of Scott et al. (1989) showed that when the frequent stimuli were omitted from the stimulus sequence, therefore changing the sequential probability of the target, the amplitude of the P3b elicited by the target was unaffected. Scott et al. inferred from this that the apparent effect of sequential probability in the study of Squires et al. appeared to be due to the simultaneous manipulation of temporal probability in that study. In the present experiment, as in the study of Squires et al. (1976), changing the stimulus sequence

changed both sequential and temporal probability. The finding that local stimulus sequence does not have an effect on the P3b is, therefore, difficult to explain. It is possible that the changes in subjective probability were not large enough, in the present experiment, to affect the amplitude of the P3b.

The mean amplitude of the P3a was found to be significantly larger in response to a novel sound immediately preceded by several frequent stimuli (5FT-N) and a novel sound preceded by an identical novel sound and a frequent stimulus (N-F-N) than in response to a novel sound immediately preceded by an identical novel sound (N-N). The difference in amplitude between the former two conditions was not statistically significant but the trend of the means was in the predicted direction showing that a larger P3a was elicited by a stimulus preceded by several frequent stimuli (5FT-N) than by a stimulus which was preceded by an identical novel stimulus and a frequent stimulus (N-F-N). This pattern of results is consistent with Naatanen (1990). When the novel sound of interest is preceded by a number of presentations of the frequent tone, sensory memory will contain a trace of the frequent stimulus but due to the long interval since the last presentation of the novel sound, a trace of the novel sound will not be present in sensory memory. The presented novel sound will, therefore, mismatch with the trace of the frequent stimulus eliciting an MMN and subsequent N2b and P3a. If a novel sound has been recently presented, for example in the condition in which the stimulus of interest is preceded by an identical novel sound and a frequent tone, sensory memory will contain a trace of the frequent stimulus but a weak trace of the novel sound will also be present. The presented novel sound will mismatch with the trace of the frequent stimulus but match that of the novel sound. The mismatch will be greater than the match so an overall mismatch will be detected which will be reflected by the elicitation of an MMN and the elicitation of an N2b and P3a. The N2b and P3a only occur if the mismatch is

sufficiently large to overcome a threshold proposed by Naatanen (in prep) to exist between the MMN and N2b generator mechanisms. As the magnitude of the N2b process is thought to be dependent on the size of the mismatch, a smaller N2b and subsequent P3a would be expected shortly following the presentation of a novel sound than when the stimulus is preceded by a number of frequent stimuli. When the novel sound of interest is immediately preceded by an identical novel sound a stronger trace of the novel sound will be present in sensory memory than in the condition in which there is an intervening frequent. The resultant mismatch produced will be smaller than that produced in the intervening frequent condition because the mismatch with the trace of the frequent will occur but a larger match will occur with the trace of the novel sound (because the trace of the novel sound is stronger than in the preceding condition).

The decrease in amplitude over the three conditions, of the deflection labelled here as the P3a, did not differ between sites in the analysis in which all electrode sites were included. The separate ANOVAs performed at frontal and parietal sites, however, revealed different patterns of amplitude change occurring at the front and back of the head. The ANOVA on the novel P300 deflection at frontal sites showed no significant difference in amplitude between conditions. At parietal sites a significant condition effect was obtained, the novel sound preceded by at least five non-novel sounds elicited a larger P3a than that elicited by a novel sound immediately preceded by a novel sound. This pattern of amplitudes is as predicted in the Introduction for the effect of stimulus sequence on the P3a. The distribution of the effect is not, however, consistent with the effect occurring on the anteriorly distributed P3a component but suggests instead that sequence may be having its effect on a more posteriorly distributed component contributing to the novel P300 deflection, possibly the P3b. It is therefore surprising that sequence did not have a

significant effect on the amplitude of the P3b elicited by the targets. It is possible that access to processing which allows conscious discrimination of the stimulus can be achieved by several different routes (e.g. Naatanen, 1990 who discusses automatic and controlled routes to conscious discrimination) and that the targets and novel sounds are taking different routes to conscious discrimination. An alternative explanation is also possible. It has been suggested that the P3a reflects a necessary preliminary process for the occurrence of the orienting response (Loveless, 1983; Naatanen, 1990) and the P3b reflects processes occurring subsequent to the orienting response (Naatanen, 1990). On repeated presentation of a novel sound (to which no response is required) less orienting would occur (Sokolov, 1960, 1963), which Bernstein and Taylor (1979) has suggested is due to the subjects realising that the novel sounds had no relevance for the task. The results of the present experiment could, therefore, be explained by suggesting that because there is a decrease in the orienting response to the novel sound, there is a corresponding decrease in the amplitude of the P3a and the P3b. It is however, difficult to explain why the posteriorly distributed P300 component is affected more by repetition of the novel sound than the more anteriorly distributed P3a. As the targets are significant for the task in that they require a button press and the orienting response to significant stimuli has been reported to show little habituation (Sokolov, 1960, 1963), repeated presentation of the target stimulus would not be expected to affect the amplitude of the P3b elicited by the targets.

Single trial analysis of P3a

The scalp distribution of the P3a measured in the single trials confirmed that the novel P300 measured in the single trials and the averaged waveforms was the same deflection. The P3a elicited at Cz and Pz differed across trials differently from that

elicited at Fz. The amplitude of the P3a elicited at Cz and Pz was larger than that elicited at Fz over all trials. For trials 9-12 this difference between sites was larger than that on earlier trials. The increased difference was obtained because the amplitude of the P3a increased at Cz and Pz on trials 9-12 but no change in amplitude was found at Fz. The increase in amplitude was found to occur as a step increase at Cz and Pz from trial 8 to trial 9. The results of the analysis of the novel P300 deflection in the single trials suggests that, unlike the reports of Courchesne et al. (1975), Courchesne (1978), Knight (1984) and Yamaguchi and Knight (1991a), there appears to be no decrease in amplitude of the novel P300 elicited at Fz over the first few presentations of the novel stimulus. There is an increase, however, in amplitude of the novel P300 at Cz and Pz from trial 9 onwards, compared with previous trials, which is consistent with the reported increase in amplitude of the novel P300 at posterior sites over trials. It is uncertain why this increase in amplitude occurred so abruptly and why it occurred between trials 8 and 9 in particular. The increase in amplitude at central and parietal sites may be reflecting increased activity of the generator producing the posteriorly distributed P300 on repeated presentation of the novel sound (see Courchesne (1978) who has suggested that the parietal shift of the P300 deflection may represent the evolution of categorisation rules to the novel stimuli).

N100

The N100 elicited by the target tones and the novel sounds had a similar scalp distribution to that elicited by these stimuli in the other experiments reported here. Both categories of rare stimuli elicited an N100 which was of maximal amplitude over frontal and central sites. The previous experiments reported here suggest that the rare tones elicit a fronto-centrally maximal N100, whereas the novel sounds

elicit a centrally maximal N100. It is uncertain why the distribution between conditions was found not to differ in the present experiment. No significant differences in N100 latency or amplitude were found between the two categories of rare stimuli or between the three conditions. Even when the analysis was confined to frontal sites and only to the N100 elicited by the novel sounds, where the grand averaged waveforms suggested the possible presence of a refractory effect, no differences in N100 amplitude were found between conditions. The result suggests that the local sequence of stimuli had no significant effect on N100 amplitude. This is consistent with Naatanen's hypothesis that the N100 is elicited prior to accessing sensory memory. It is surprising, however, that there is no decrease in amplitude of the N100 on immediate repetition of stimuli because at least some of the generators contributing to the activity in the N100 region are thought to be refractory (Naatanen and Picton, 1987).

P170

As in previous experiments reported here, the apparent scalp distribution of the P170 was affected by the P300 on which it was superimposed. The P170 elicited by the targets had a centro-parietal maximum at the midline and a parietal maximum at lateral sites whereas that elicited by the novel sounds had a central maximum over all electrode chains. For both categories of rare stimuli, the P170 was significantly larger at central and parietal sites than at frontal sites when the rare stimulus was immediately preceded by the identical rare stimulus. No significant differences between sites were found for the other conditions. The P170 is less affected by P300 overlap at frontal sites than at central and parietal sites, so a separate analysis was performed on the P170 elicited by targets and novels at frontal sites only. No significant effects of stimulus or condition were found. The P170, therefore, appears

to be unaffected by the local stimulus sequence. This suggests that the P170 may be reflecting a process prior to the mismatch detection process proposed by Naatanen to elicit the MMN.

A problem for the interpretation of the amplitude of the P170 and P300 deflections elicited by a novel sound immediately preceded by an identical novel sound, is that there appears to be a negative shift of this region of the waveform compared with the same region of the waveform elicited by stimuli in the other two conditions. There are two possible explanations for this effect. This apparent shift may be produced because both the P170 and P300 are smaller in response to the novel sounds in this condition compared with the other two conditions. Alternatively, in this condition a negative component may overlap the P170 and P300 in time which through summation with these components would reduce the amplitude of the P170 and P300 deflections.

400-800 ms region

The 400-800 ms latency region was used for the analysis of the present experiment because the frontal negativity and parietal positivity following the P300 deflection appears to onset at approximately 400 ms in the present experiment and inspection of the grand averaged waveforms suggest that the apparent differences between condition occur soon after 400 ms. The slightly earlier latency window, than that used to investigate the slow waves in the previous experiments reported in this thesis (500-900 ms), therefore ensured that we captured these modulations of the waveform by the stimulus conditions. The results of the analyses showed that the 400-800 ms region elicited by both the novel sounds and the targets did not differ significantly between conditions at frontal sites. For the targets there was a slight

difference in distribution between conditions at frontal sites, the targets when preceded by a frequent elicited a 400-800 ms region which was of maximal amplitude over midline and the left hemisphere compared with the midline maximum of the 400-800 ms region elicited by a target immediately preceded by a target. At parietal sites the 400-800 ms region elicited by a novel sound immediately preceded by a novel sound, and a novel sound preceded by a novel sound and intervening frequent tone, was significantly less positive than that elicited by a novel sound preceded by at least five non-novel sounds. For the targets, the 400-800 ms region was more positive in the two conditions in which the target was preceded by a frequent stimulus than in the condition in which the target was immediately preceded by a target.

These results therefore provide further evidence in support of the dissociation of a frontal negative and parietal positive slow wave. The frontal negative slow wave appears not to be affected by stimulus sequence. In contrast, the posterior positive slow wave appears to be affected by stimulus sequence and to be affected differently depending on whether the eliciting stimulus is a target or a novel sound. For both targets and novel sounds, however, the 400-800 ms region elicited by a rare stimulus preceded by at least five non-identical stimuli was significantly larger in amplitude than that elicited by a rare stimulus immediately preceded by an identical stimulus. The difference between stimuli appears to be whether the amplitude of the 400-800 ms region elicited by the rare stimuli preceded by an identical rare stimulus and intervening frequent is more positive than that of the other two conditions or has an amplitude midway between the two. The findings suggest that the frontal slow wave may be reflecting further processing of rare stimuli whereas the posterior slow wave may be reflecting further processing of rare stimuli but that the extent of this processing may depend on whether the stimulus has recently been presented or not.

Summary of findings

The amplitude of the P3b component of the P300 complex elicited by rare target stimuli was unaffected by the order of stimuli in the local part of the stimulus sequence. This is inconsistent with previous reports of the effects of subjective probability on P3b amplitude and is difficult to explain. The amplitude of the P300 deflection elicited by novel sounds was found to be larger when the novel sound was preceded by several frequently occurring stimuli than when it was preceded by an identical novel sound. This finding is consistent with the proposals of Naatanen (1990) that the P300 deflection elicited by a rare non-target stimulus results from the detection of a mismatch between the features of the presented stimulus and those of previous stimulation represented in the sensory memory trace. The finding that the effect of local stimulus sequence on P300 deflection amplitude was not restricted to anterior sites suggests that both P3a and P3b components, whose overlapping activity are thought to produce the novel P300 deflection, may be affected. In fact separate analyses of the novel P300 at frontal and posterior sites suggest that sequence may be having its effect mainly at posterior sites. This suggests that the effect of local stimulus sequence may be on the posterior contribution to the novel P300 deflection (P3b), which is difficult to explain in terms of Naatanen's theory. The analysis of the P300 deflection elicited by the novel sound in the single trials showed that there was no significant habituation of the deflection from the second to the twelfth presentation of the novel stimulus which is inconsistent with previous reports and suggests that the anteriorly distributed P3a component does not show habituation and is not a sign of the orienting response in the way that autonomic measures are. The increase in amplitude of the P300 deflection over central and posterior sites from the ninth presentation of the novel sound onwards may be

reflecting increased activity of the P3b generator on repeated presentation of the novel sound.

CHAPTER 11

SUMMARY OF FINDINGS AND GENERAL CONCLUSIONS

SUMMARY OF NAATANEN'S THEORY

As the results of the experiments reported in this thesis were interpreted in terms of Naatanen's theory (1990), I will briefly summarise the theory before turning to the summary of experimental findings and conclusions.

Naatanen proposed that in a one channel oddball task, attentional discrimination of stimuli is initiated by a preattentional process which detects a mismatch between the physical features of the presented stimulus and a *passively* formed sensory memory trace representing the physical features of stimuli which have been recently presented. The mismatch detection, reflected by the mismatch negativity (MMN), activates a process reflected by the N2b. If the processing reflected by the N2b is activated to such an extent that it overcomes a certain threshold, it causes an attentional switch allowing the stimulus access to "central executive mechanisms". The P3a is suggested to be related to the attentional switch.

The second part of Naatanen's model concerns parallel controlled processing as an alternative route to attentional processing. This route involves the detection of a match between the presented stimulus and an *actively* formed trace of the features of the attended stimulus. Naatanen does not consider the controlled processing route to be that used for target detection in a one channel oddball task, as he suggests that the target stimuli do not occur frequently enough for an attentional trace of their physical features to be maintained.

SUMMARY OF P300 COMPLEX FINDINGS

Experiment 1. The aim of the experiment was to replicate the previously reported dissociation of the P300 complex into P3a and P3b components (Knight et al., 1989). Subjects were presented with a slightly modified version of the paradigm used by Knight et al.. Two 300 trial stimulus sequences were presented consisting of the random mixing of a frequent tone (P=0.70), a rare target tone (P=0.15), requiring a response, and a rare novel sound (P=0.15). The same probabilities of frequent, rare target and rare nontarget stimuli were used in the subsequent experiments.

Both categories of rare stimuli elicited a P300 deflection which was not elicited by the frequent stimuli. This finding supports the previously reported inverse relationship between stimulus probability and P300 amplitude. Target tones were found to elicit a P3b component which was distributed maximally over parietal sites for all electrode chains. In contrast, the novel sounds elicited a slightly earlier P3a component which was maximally distributed over centro-parietal sites at the midline but had a parietal maximum at lateral sites. These results were consistent with the previously reported dissociation of the auditory P300 complex.

There are two possible explanations for the difference in scalp distributions of the P3a and P3b. The two deflections may reflect the activity of independent generators, one exclusively activated by novel sounds, the other activated by target tones. Alternatively, the same generators could be activated by both categories of rare stimuli but to different extents.

Experiment 2. The results of this experiment showed that when the rare non-target was either a tone in a sequence of frequent and rare target tones or a novel sound in a sequence of frequent and rare target novel sounds, it did not elicit a P3a (defined as a P300 deflection with a centro-parietal maximum). A P300 deflection was elicited by the rare non-target stimuli but this was distributed maximally over parietal sites in the same way as the P3b elicited by the target tones and target novel sounds.

The results of experiment 2 suggest that not all rare non-target stimuli elicit a P3a. Although the rare non-targets deviated from the frequent stimuli, it appears that this deviation was not large enough to trigger attentional processing. This is consistent with Naatanen's proposal that attentional processing will only be triggered if the mismatch is large enough to exceed a threshold. The results also suggest that a P3a is not elicited by all novel sounds. This is consistent with Naatanen's view that a P3a is produced as a result of a comparison between the presented stimulus and a trace of the features of previously presented stimuli.

Experiment 3. Subjects were presented with one of the stimulus sequences from experiment 1 and instructed to respond to the rare novel sounds but not to the rare tones. This allowed the investigation of two hypotheses. (1) The first hypothesis was based on an interpretation of the strategy used in experiment 1. In that experiment the frequent stimuli may have been ignored because of their predictability, leaving a go/no-go response to be made to the two categories of rare stimuli. As both categories of rare stimuli were relevant to the task, in that they both required some kind of response (press a button/inhibit a button press), both would be expected to elicit a P3b. The centro-parietal distribution of the P3a, elicited by novel sounds, was suggested to have resulted from the overlap of a P3b and more anterior (P3a) activity elicited by detection of a mismatch between a sensory memory trace

and the presented 'novel' stimulus. If this were the case, the same scalp distribution would be expected in response to the novel sounds when they are targets (experiment 3) compared with when they were rare nontargets (experiment 1). (2) A second hypothesis comes from the findings of a number of studies that "no-go" stimuli elicit a centro-parietally distributed P300 and "go" stimuli elicit a parietally distributed P300 deflection. If the centro-parietal distribution of the P3a reflects the activation of a no-go generator when the novel sounds are nontargets, a parietally distributed P300 deflection would be predicted in response to the novel sounds when targets ("go" stimuli).

A P300 deflection with a centro-parietal maximum was elicited by the target novel sounds but this was more posteriorly distributed than that elicited by the rare nontarget novel sounds in Experiment 1. The amplitude and distribution of the P300 elicited by target novel sounds suggested there was a contribution of activity to the waveform additional to that involved in generating the P3b to target tones. The centro-parietal distribution of the P300 to novel sounds in experiment 1 was proposed to result from the overlap of posterior and more anterior activity. The parietal shift in distribution of the P300 deflection elicited by rare nontarget novel sounds in the present experiment may have been due to the generators producing the posterior and anterior activity being activated to different extents in the two experiments. The rare non-target tone did not elicit a P300 deflection. It is possible that the rare tone may have been grouped with the frequent tones to form one category of tones with high probability of occurrence. This category of tones may then have been treated as no-go stimuli but because of their high probability would have elicited only a very small P300, if any.

Neither of the two hypotheses was clearly supported by the experimental results. The change in distribution of the P300 from a centro-parietal to a parietal maximum, which occurred when the novel sounds became targets, may suggest the activation of a "go" generator by the target novel sounds. The P300 deflection to target novel sounds was, however, more anteriorly distributed than that elicited by the target tones suggesting that differences in relative strengths of the activity of P3a and P3b generators may be causing the differences in distribution.

Experiment 4. Omission of the frequent stimuli from the sequence used in experiment 1 was found to abolish the P3a elicited by the novel sounds but not to affect the P3b elicited by the target tones. A parietally distributed P300 deflection was elicited by the rare non-target novel sounds when the frequents were omitted.

In this task it was not possible to use the mismatch detection route to gain access to central executive processes because the representation of the features of a stimulus in sensory memory would have decayed by the next presentation of the stimulus. The results of the present experiment support Naatanen's proposal that a process detecting mismatches between presented stimuli and a short duration trace of previous stimuli is necessary for the elicitation of the P3a but is not necessary for the elicitation of the P3b. The P3b is thought to be elicited after the stimulus has received processing by the central executive mechanisms. Mismatch detection is probably one of several routes available for accessing central executive mechanisms.

Experiment 5. Subjects were presented with a stimulus sequence in which the frequent and rare target stimuli were two different novel sounds and the rare nontarget stimulus was a tone. The frequent novel sounds did not elicit a P300

deflection. In contrast, both the target novel sound and the rare nontarget tone elicited a parietally distributed P300 deflection.

The results of the present experiment appear to be inconsistent with Naatanen's theory. The same stimuli were used in experiments 1, 5 and 6. The experiments differed only in the reversal of the conditions to which the stimuli were assigned. The rare nontarget in experiment 5 deviated from the frequent stimuli to the same extent as experiments 1 and 6 in which the rare nontarget elicited a P3a. The results suggest that the magnitude of the mismatch with the trace of the frequent stimuli does not appear to be the only factor determining the occurrence of a P3a.

Experiment 6. Subjects were presented with one 800 trial stimulus sequence. The sequence consisted of the random mixing of a frequent tone, a rare target tone requiring response, and a rare novel sound. Two novel sounds were presented as rare nontargets in the stimulus sequence. One novel sound was used in the first 400 trials but was replaced by a different novel sound in the next 200 trials. For the final 200 trials, the novel sound used in the first 400 trials was again presented as the rare nontarget. This allowed investigation of habituation and dishabituation of the P3a component.

The results showed that when a single novel sound is presented as the rare non-target, it elicits a P3a with the same scalp distribution as that elicited when the rare nontarget is a category of several different novel sounds. This suggests that in order for a stimulus to elicit a P3a it does not have to be novel in the sense that it has not been heard before. The P3a was found not to differ significantly in amplitude between the blocks of trials, although there was a trend for the means to decrease as predicted. Although the P3a did not habituate across the entire sequence,

habituation of the P3a may have occurred rapidly over the first few presentations of the novel sound. The results suggest that, whereas the P3a may be related to the orienting response (OR), it does not appear to be a sign of the OR in the same way as autonomic measures. This is consistent with the view of Naatanen that the P3a may be related to, but not necessarily a reflection of, the OR.

Experiment 7. The effect of local stimulus sequence on the amplitude of the P3a was investigated. Subjects were presented with a sequence of 600 stimuli consisting of the random mixing of a frequent tone, a rare target tone and a novel sound. Three conditions were investigated for both the targets and novel sounds. The conditions included (a) a rare stimulus immediately preceded by the identical rare stimulus (X-X), (b) a rare stimulus preceded by an identical rare stimulus and an intervening frequent stimulus (X-F-X) and (c) a rare stimulus preceded by at least five nonidentical stimuli (5F-X) (where X refers to the rare stimulus, F refers to the frequent stimulus and 5F refers to frequent stimuli and rare stimuli other than the category of interest). If the mismatch process proposed to be necessary for the elicitation of the P3a (Naatanen, 1990) occurs with a short duration trace, only the features of recently occurring stimuli would be expected to be represented in the trace. Thus, the amplitude of the P3a should be larger in condition (c) compared with conditions (a) and (b).

The amplitude of the P3b elicited by rare target stimuli was unaffected by the local stimulus sequence. This finding is inconsistent with the findings of Squires et al. (1976). The amplitude of the P300 deflection elicited by novel sounds was found to be larger when the novel sound was preceded by several frequently occurring stimuli than when it was preceded by an identical novel sound. This finding was not restricted to anterior sites. The analysis of the P300 deflection elicited by the novel

sound in the single trials showed that there was no significant habituation of the deflection over the first 12 presentations of the novel stimulus.

The effects of local stimulus sequence suggest that the P300 deflection elicited by rare nontarget novel sounds in the present experiment results from the detection of a mismatch between the features of the presented stimulus and those of recently presented stimuli represented in a short duration sensory memory trace. The finding that the effect of local stimulus sequence on the amplitude of the novel P300 deflection was not restricted to anterior sites suggests that both P3a and P3b components, whose overlapping activity are thought to produce the deflection, appear to be affected. This is difficult to explain in terms of Naatanen's theory which predicts that only the P3a should be affected by local stimulus sequence.

The absence of habituation of the P3a component in the single trials is inconsistent with previous reports and provides a further indication that the P3a component is not a sign of the orienting response in the same way as autonomic measures.

KNOWLEDGE ABOUT THE P3A OBTAINED FROM THE PRESENT EXPERIMENTS AND POSSIBLE FUTURE INVESTIGATIONS

Three main findings have emerged from the experiments reported in this thesis which increase our knowledge of the P3a component.

(1) The striking stability of the P3a component. The P3a continues to be elicited with no significant decrease in amplitude after a number of presentations of the eliciting stimulus. This has important implications for proposals relating P3a to the

orienting response. The lack of habituation of the P3a suggests that this component does not reflect or follow the orienting response, though it may precede it.

The stability of the P3a also makes implications for theories of orienting reflex (OR). It suggests that habituation of the orienting response occurs at a stage of processing subsequent to detection of a mismatch and call for an attentional switch, in as much as these processes are reflected by the P3a.

An interesting series of experiments could be carried out to clarify further the relation between the P3a component and the OR. These experiments could involve the recording of both ERPs and autonomic nervous system activity in order to determine the degree of correspondence between the P3a and autonomic measures of orienting. The P3a may be a precursor of the OR and thus a necessary but not sufficient condition for the genesis of the OR. It could be predicted from this, that the autonomic indicators of the OR would always be accompanied by a P3a but the reverse would not necessarily be true.

(2) The functional distinction between P3a and P3b. The omission of frequent stimuli was found to selectively affect the P3a whilst leaving the P3b unaffected. This finding therefore suggests a functional distinction between the P3a and P3b. This supports the identification of the P3a and P3b as separate components; a dissociation which has previously been made only on the basis of differences in scalp distribution (Squires et al., 1975; Knight, 1984; Knight et al., 1989) and differential effects of brain lesions (Knight, 1984; Knight et al., 1989).

(3) A physical mismatch between input and memory is necessary but not sufficient to elicit the P3a. Omission of the frequent stimuli from the sequence suggested that

a comparison between the rare 'novel' sounds and the sensory memory representation of frequent stimuli was necessary to elicit the P3a. The results suggested that the detection of a mismatch during this comparison was a necessary condition for eliciting the P3a. Other experiments, however, suggested that mismatch detection was not a sufficient condition for P3a elicitation.

According to Naatanen's theory, the P3a is generated by a mismatch between an input stimulus and a stored representation (of the frequently occurring nontarget). In experiment 1 the input stimulus for this comparison process was a novel sound and the passively created representation was a tone. In experiment 5 the situation was reversed, the input was a tone and the representation was a novel sound. Obviously the physical mismatch between input and representation was identical in the two experiments, yet only experiment 1 produced a P3a.

To explain these results it is necessary to postulate additional factors influencing attentional switch. It is possible that certain types of stimuli are inherently more salient and that these facilitate a switching of attention. For example, the input stimulus characteristics (e.g. the fast rise time of novel sounds) may lower the threshold which the mismatch needs to overcome for attentional switch. This interpretation could be tested by seeing whether novel sounds with slower onset time produce a P3a when presented as rare nontargets.

Finally, another approach to furthering our knowledge about the P3a would be the investigation of the effects of disruption of neurotransmitter systems, whether through disorders or through the administration of drugs. This could provide further information concerning the degree of dissociation of the P3a and P3b components.

For example different neurotransmitters may selectively affect the generation of the one component.

IMPLICATIONS OF THE PRESENT FINDINGS FOR NAATANEN'S THEORY

The findings of the experiments reported in this thesis support Naatanen's suggestion that there appears to be a route to attentional processing which depends on the detection of a mismatch between the presented stimulus and a short duration sensory memory trace of previously presented stimuli. The P3a appears to be related to the resulting attentional switch. Contrary to the proposals of Naatanen, a quantitative mismatch appears not to be sufficient to elicit a P3a (as described above).

Also contrary to Naatanen's proposal, the mismatch detection route appears not to be that necessarily taken in a one channel oddball task to access central executive mechanisms. The rare tones appear to gain access to attentional processing via a different route, as these stimuli do not elicit a P3a. The alternative route may involve the detection of a match between the presented stimulus and a representation of the stimulus to be attended. This would be similar to the controlled processing route proposed by Naatanen.

The differences in scalp distribution of the P300 elicited by the novel sounds assigned to different experimental conditions, and the difference in distribution of the P300 deflection elicited by tones and novel sounds assigned to the same condition, may reflect differing contributions to the waveform of the activity of P3a and P3b generators. The novel sounds appear to activate processing reflected by the

P3a, whereas this appears not to be activated by rare tones. This is inconsistent with Naatanen's proposal that the P3a should be elicited by all rare stimuli.

In summary, the results suggest that mismatch detection appears to be one route to attentional processing (consistent with Naatanen, 1990) but that this is not necessarily the only route taken in a one channel oddball task (inconsistent with Naatanen, 1990).

WHAT HAS BEEN LEARNT ABOUT OTHER ERP COMPONENTS FROM THE PRESENT EXPERIMENTS?

N100. The N100 elicited by the tones was found to be differently distributed over the electrode sites from that elicited by the novel sounds, irrespective of the condition to which these stimuli belonged within the task. This difference in distribution may reflect the contribution to the waveform of different N100 components in response to the two categories of stimuli. The results suggest that the N100 was more dependent on the physical aspects of the stimuli than on task variables. The independence of the N100 deflection from the variables manipulated in the tasks used in this thesis is consistent with Naatanen's view that it reflects activity of a transient-detector system which sends interrupt signals to "central executive mechanisms".

P170. The P170 was always found to be larger in amplitude in response to novel sounds compared with rare tones irrespective of the experimental conditions. The difference in amplitude of the P170 between novel sounds and tones may be due to a physical difference between the stimuli, for example, stimulus duration. The results

of experiment 5 question this interpretation. In this experiment a larger amplitude P170 was found in response to a rare novel sound as compared with a frequently occurring novel sound despite the fact that these two novel sounds shared many physical characteristics. The interpretation is complicated by the suggestion that the P170 is made up of two components. In Chapter 4 it was suggested that the P170 deflection elicited by the rare stimuli results from the overlap of a P200 component elicited by all attended stimuli and a P165 (identified by Goodin et al., 1978) elicited by rare attended stimuli. It is possible that the difference in amplitude between frequent and rare sounds in experiment 5 was produced because the P170 elicited by the rare novel sounds comprised overlapping P165 and P200 components, whereas that elicited by the frequent novel sounds may have reflected only the contribution to the waveform of a P200 component. The longer latency of the P170 elicited by frequent stimuli supports the interpretation.

The superimposition of the P170 deflection on the rising slope of the P300 deflection made the investigation of differences in amplitude and scalp distribution between conditions difficult. The P170 was not dependent on the detection of a mismatch with a trace of the frequently occurring stimuli, as this deflection was found in response to rare stimuli when the frequent stimuli were omitted (experiment 4) and was unaffected by stimulus sequence (experiment 7). The results suggest that the P170 may reflect a response to attention capturing stimuli but that this processing is not dependent on a stimulus comparison process.

MMN/N2b. These components are of importance for the evaluation of Naatanen's theory. When stimuli are attended, the MMN and N2b components summate producing an N200 deflection. When the stimulus sequence is ignored the N2b is absent. In the present series of experiments the N200 deflection was superimposed

on the rising slope of the P300 deflection. In the experiments reported in this thesis it was not possible, therefore, to obtain a useful measure of the amplitude of this negative deflection. As all the experiments reported in this thesis required the subject to attend to the stimulus sequence, even if a measure of the amplitude of the N200 deflection had been obtained, it would not have been possible to distinguish the effect of variable manipulations on the MMN and N2b components.

P3b. The P3b was elicited by all rare target stimuli and also by some rare nontarget stimuli. Rare nontargets produced a P3b when they shared certain characteristics with the frequent stimuli (for example, a rare nontarget novel sound presented within a sequence of novel sounds). The occurrence of the component was unaffected by omission of the frequently occurring stimuli, suggesting that a mismatch detection process was not necessary for its elicitation. This result is consistent with Verleger's theory (1988) which proposes that the P3b is elicited by the closure of an expected event (the target). According to Verleger's theory the presence/absence of the frequent stimuli should not affect the subjects' expectancy of the target.

The results of the stimulus omission experiment are, however, inconsistent with Donchin's theory. Donchin suggests that a P3b is elicited when an updating of context is required on presentation of unexpected or significant stimuli. Donchin and Fabiani (1992) suggest that context updating involves marking attributes of an event which make it distinctive from other events which have occurred and that the extent of this updating is directly related to P3b amplitude. If there has been a period of silence before a stimulus is presented, context updating will be simple, because all the features of the stimuli will be distinctive. If, however, there is a change from presentation of one stimulus (the frequent) to another stimulus (e.g. the target) context updating in response to the latter stimulus may require more

processing because it will be necessary to extract the features of the target which make it distinctive from the frequents. A larger amplitude P3b would therefore be expected in response to the targets when the frequents are present in the sequence than when they are omitted. This was not found.

The results of the experiments reported in this thesis are consistent with the suggestion that the P3b reflects further processing of task relevant stimuli which occurs after the stimulus has gained access to central executive processing irrespective of the route taken. As the experimental manipulations were concerned with the investigation of the P3a, the P3b results were not sufficient to fully evaluate theories of the functional significance of the P3b.

Slow waves (500-900 ms region). Frontal negative and posterior positive slow waves were obtained in response to both frequent and rare stimuli but were larger in amplitude in response to the rare stimuli. The different distribution of the 500-900 ms region across electrode chain at frontal and parietal sites provided support for the identification of these deflections as separate components. The slow wave appears to reflect further processing of stimuli subsequent to that reflected by the P3b.

CONCLUSION

The findings suggest that the P3a is elicited by auditory stimuli which deviate to a sufficient extent from the frequently occurring stimuli in a sequence and which do not require a specified response. The amplitude of the P3a is sensitive to local stimulus sequence but appears not to show habituation over a sequence of stimuli.

The functional significance of this component is at present uncertain but it does appear to be related to the switching of auditory attention.

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APPENDIX

Table 4.7. ANOVA summary table for analysis of the amplitude of the N100 elicited by frequent, target and rare non-target stimuli for the two testing stimulus sequences, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	2.47	0.145
Condition (CC)	1.1,12.5	2.16	0.167
Chain (CH)	1.9,20.5	34.82	0.000*
Site (ST)	1.2,13.4	15.84	0.001*
SE*CC	1.3,14.0	0.59	0.493
SE*CH	1.7,18.3	0.53	0.564
SE*ST	1.7,18.3	2.20	0.146
CC*CH	2.5,27.1	0.78	0.489
CC*ST	2.1,23.0	14.88	0.000*
CH*ST	2.6,28.8	2.66	0.074
SE*CC*CH	2.5,27.9	0.68	0.549
SE*CC*ST	2.5,27.5	1.29	0.296
SE*CH*ST	3.7,40.4	1.72	0.170
CC*CH*ST	3.9,43.4	1.29	0.291
SE*CC*CH*ST	3.5,38.0	0.83	0.501

RESCALED AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	0.00	0.998
Condition (CC)	1.2,13.2	0.82	0.401
Chain (CH)	1.9,20.9	35.84	0.000*
Site (ST)	1.2,13.3	15.88	0.001*
SE*CC	1.4,14.9	0.03	0.915
SE*CH	1.9,20.9	0.31	0.725
SE*ST	1.6,17.6	0.11	0.853
CC*CH	2.6,29.0	0.40	0.728
CC*ST	2.2,23.8	14.05	0.000*
CH*ST	2.6,28.6	2.61	0.079
SE*CC*CH	2.7,30.1	0.58	0.618
SE*CC*ST	2.8,30.4	0.55	0.635
SE*CH*ST	3.8,42.1	1.21	0.322
CC*CH*ST	4.0,44.0	0.78	0.540
SE*CC*CH*ST	3.6,39.6	0.66	0.609

* indicates statistical significance at the 0.05 level or better

Table 4.8. ANOVA summary table for analysis of the amplitude of the P170 elicited by frequent, target and rare non-target stimuli for the two testing stimulus sequences, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	0.06	0.814
Condition (CC)	1.3,14.6	3.55	0.070
Chain (CH)	1.6,17.8	13.37	0.001*
Site (ST)	1.4,15.7	5.04	0.029*
SE*CC	1.6,17.6	0.20	0.775
SE*CH	1.3,14.8	0.41	0.591
SE*ST	1.6,17.1	1.73	0.210
CC*CH	2.3,25.6	0.18	0.863
CC*ST	2.1,23.6	3.54	0.043*
CH*ST	2.8,31.1	12.19	0.000*
SE*CC*CH	2.4,26.0	0.58	0.595
SE*CC*ST	1.5,17.0	0.77	0.444
SE*CH*ST	1.9,21.0	2.08	0.152
CC*CH*ST	4.4,47.9	2.40	0.059
SE*CC*CH*ST	4.3,47.8	0.80	0.540

RESCALED AMPLITUDE			
Factors	df	F	Prob
Sequence (SE)	1,11	0.07	0.793
Condition (CC)	1.2,13.6	0.03	0.910
Chain (CH)	1.6,17.9	12.83	0.001*
Site (ST)	1.4,15.6	4.44	0.041*
SE*CC	1.4,15.2	0.11	0.821
SE*CH	1.3,13.9	0.20	0.715
SE*ST	1.5,16.2	1.24	0.304
CC*CH	2.2,24.4	0.19	0.852
CC*ST	2.0,21.8	3.03	0.070
CH*ST	2.8,30.8	12.50	0.000*
SE*CC*CH	2.0,22.4	0.15	0.868
SE*CC*ST	1.7,18.5	0.83	0.429
SE*CH*ST	2.0,22.4	3.42	0.050*
CC*CH*ST	4.2,46.0	3.11	0.023*
SE*CC*CH*ST	4.1,44.9	1.64	0.181

* indicates statistical significance at the 0.05 level or better

Table 4.11. ANOVA summary table for analysis of the amplitude of the 500-900 ms region elicited by frequent, target and rare non-target stimuli for the two testing stimulus sequences, before and after rescaling

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Sequence (SE)	1,11	0.97	0.344	Sequence (SE)	1,11	0.21	0.657
Condition (CC)	1.2,13.3	0.52	0.516	Condition (CC)	1.5,16.1	0.06	0.898
Chain (CH)	1.8,19.9	1.53	0.242	Chain (CH)	1.8,19.3	0.87	0.419
Site (ST)	1.3,14.8	62.11	0.000*	Site (ST)	1.8,19.3	30.27	0.000*
SE*CC	1.9,21.4	0.17	0.837	SE*CC	1.1,12.3	0.28	0.633
SE*CH	1.7,18.9	1.18	0.325	SE*CH	2.0,21.5	2.80	0.084
SE*ST	1.5,16.7	1.22	0.310	SE*ST	1.2,13.3	1.62	0.231
CC*CH	2.1,23.6	2.31	0.119	CC*CH	2.0,21.8	0.74	0.487
CC*ST	1.3,14.6	12.79	0.002*	CC*ST	1.4,15.2	0.81	0.418
CH*ST	2.6,29.1	9.21	0.000*	CH*ST	2.7,29.4	6.73	0.002*
SE*CC*CH	2.9,32.2	0.35	0.781	SE*CC*CH	1.8,20.0	2.37	0.123
SE*CC*ST	2.6,28.5	0.15	0.911	SE*CC*ST	1.4,15.9	1.27	0.296
SE*CH*ST	3.1,33.7	1.63	0.202	SE*CH*ST	2.2,23.9	0.38	0.706
CC*CH*ST	4.6,50.2	4.86	0.001*	CC*CH*ST	2.7,29.6	2.70	0.069
SE*CC*CH*ST	3.6,39.8	1.44	0.242	SE*CC*CH*ST	2.6,28.1	0.56	0.617

* indicates statistical significance at the 0.05 level or better

Table 5.4. ANOVA summary table for analysis of the amplitude of the N100 elicited by frequent, target and rare non-target stimuli for the two tasks, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	0.00	0.953
Condition (CC)	1.7,18.6	3.44	0.060
Chain (CH)	1.3,14.5	47.90	0.000*
Site (ST)	1.4,14.9	35.89	0.000*
TA*CC	1.7,18.2	0.31	0.693
TA*CH	2.0,21.9	0.08	0.925
TA*ST	1.4,15.1	4.54	0.040*
CC*CH	2.8,30.7	3.00	0.049*
CC*ST	2.8,31.0	1.55	0.224
CH*ST	2.1,23.2	2.88	0.074
TA*CC*CH	3.0,32.7	0.52	0.669
TA*CC*ST	2.6,28.2	1.04	0.383
TA*CH*ST	2.5,27.5	2.52	0.089
CC*CH*ST	4.0,44.1	0.59	0.673
TA*CC*CH*ST	3.8,41.9	0.32	0.857

RESCALED AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	0.19	0.674
Condition (CC)	1.6,17.2	0.01	0.977
Chain (CH)	1.3,14.5	47.32	0.000*
Site (ST)	1.3,14.8	35.70	0.000*
TA*CC	1.8,19.5	0.04	0.948
TA*CH	2.0,22.0	0.04	0.958
TA*ST	1.4,15.2	5.37	0.026*
CC*CH	2.9,31.7	0.29	0.821
CC*ST	2.9,31.6	1.62	0.207
CH*ST	2.1,22.9	2.86	0.076
TA*CC*CH	2.9,31.6	0.62	0.599
TA*CC*ST	2.4,26.2	0.71	0.524
TA*CH*ST	2.5,28.0	2.54	0.085
CC*CH*ST	3.5,38.1	0.53	0.690
TA*CC*CH*ST	3.9,43.0	0.25	0.902

* indicates statistical significance at the 0.05 level or better

Table 5.6. ANOVA summary table for analysis of the amplitude of the P170 elicited by frequent, target and rare non-target stimuli for the two tasks, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	0.35	0.563
Condition (CC)	1.9,21.4	0.22	0.795
Chain (CH)	1.5,16.6	28.39	0.000*
Site (ST)	1.8,19.3	14.84	0.000*
TA*CC	1.7,18.9	0.69	0.491
TA*CH	1.9,20.6	0.35	0.698
TA*ST	1.6,17.8	1.57	0.235
CC*CH	2.8,30.7	1.73	0.186
CC*ST	2.3,25.2	1.98	0.155
CH*ST	2.6,29.0	12.17	0.000*
TA*CC*CH	3.0,32.7	0.82	0.488
TA*CC*ST	2.2,24.3	1.51	0.242
TA*CH*ST	2.8,31.1	1.24	0.313
CC*CH*ST	4.7,51.3	0.80	0.549
TA*CC*CH*ST	2.8,30.9	0.25	0.851

RESCALED AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	0.28	0.604
Condition (CC)	1.9,21.3	0.21	0.808
Chain (CH)	1.5,16.6	26.93	0.000*
Site (ST)	1.8,19.3	14.34	0.000*
TA*CC	1.7,18.2	0.12	0.849
TA*CH	1.8,20.1	0.32	0.708
TA*ST	1.6,17.6	1.62	0.228
CC*CH	2.9,31.6	2.06	0.128
CC*ST	2.4,25.9	0.77	0.491
CH*ST	2.6,28.5	11.59	0.000*
TA*CC*CH	2.8,30.8	0.19	0.889
TA*CC*ST	2.1,23.5	0.81	0.462
TA*CH*ST	2.8,31.1	1.20	0.324
CC*CH*ST	4.5,50.0	1.03	0.410
TA*CC*CH*ST	2.9,32.1	0.47	0.702

* indicates statistical significance at the 0.05 level or better

Table 5.7. ANOVA summary table for analysis of the amplitude of the N200 elicited by frequent, target and rare non-target stimuli for the two tasks, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Task (TA)	1,11	2.86	0.119	Task (TA)	1,11	0.02	0.894
Condition (CC)	1.7,18.3	2.99	0.083	Condition (CC)	1.3,14.6	0.35	0.620
Chain (CH)	1.6,17.1	27.11	0.000*	Chain (CH)	1.5,16.4	26.47	0.000*
Site (ST)	1.3,14.0	41.36	0.000*	Site (ST)	1.3,14.2	42.17	0.000*
TA*CC	1.9,21.3	1.99	0.163	TA*CC	2.0,21.7	0.24	0.785
TA*CH	1.9,20.4	2.41	0.118	TA*CH	1.8,20.3	0.96	0.392
TA*ST	1.5,16.7	1.92	0.183	TA*ST	1.4,15.1	1.64	0.226
CC*CH	2.8,31.0	2.37	0.093	CC*CH	2.5,27.4	4.61	0.013*
CC*ST	2.4,26.8	8.96	0.001*	CC*ST	2.6,28.5	4.66	0.012*
CH*ST	3.1,34.4	10.85	0.000*	CH*ST	3.1,34.6	11.82	0.000*
TA*CC*CH	2.9,32.0	1.01	0.401	TA*CC*CH	2.7,30.1	0.83	0.477
TA*CC*ST	1.6,17.4	0.61	0.515	TA*CC*ST	1.7,18.6	0.95	0.389
TA*CH*ST	3.1,34.4	3.34	0.029*	TA*CH*ST	3.2,34.8	1.96	0.136
CC*CH*ST	3.3,35.8	2.02	0.125	CC*CH*ST	3.2,35.0	2.75	0.055
TA*CC*CH*ST	3.5,38.0	0.64	0.612	TA*CC*CH*ST	3.7,40.8	0.67	0.602

* indicates statistical significance at the 0.05 level or better

Table 5.8. ANOVA summary table for analysis of the amplitude of the N200 elicited by target and rare non-target stimuli for the two tasks, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Task (TA)	1,11	0.65	0.435	Task (TA)	1,11	0.11	0.745
Condition (CC)	1,11	3.37	0.094	Condition (CC)	1,11	0.02	0.882
Chain (CH)	1.7,19.2	22.56	0.000*	Chain (CH)	1.8,19.3	21.74	0.000*
Site (ST)	1.2,13.2	37.74	0.000*	Site (ST)	1.2,13.2	37.99	0.000*
TA*CC	1,11	2.90	0.117	TA*CC	1,11	0.22	0.650
TA*CH	1.7,18.8	1.28	0.296	TA*CH	1.7,18.9	0.70	0.486
TA*ST	1.9,20.8	2.44	0.115	TA*ST	1.8,20.3	1.95	0.170
CC*CH	1.3,14.8	0.79	0.424	CC*CH	1.3,14.7	0.81	0.415
CC*ST	1.6,17.5	0.08	0.881	CC*ST	1.6,17.4	0.33	0.673
CH*ST	3.0,33.0	7.25	0.001*	CH*ST	3.0,32.9	7.18	0.001*
TA*CC*CH	2.0,21.8	1.45	0.258	TA*CC*CH	2.0,21.7	1.22	0.315
TA*CC*ST	1.2,12.9	0.31	0.624	TA*CC*ST	1.2,13.1	0.50	0.520
TA*CH*ST	2.4,26.7	2.92	0.063	TA*CH*ST	2.3,25.6	2.22	0.123
CC*CH*ST	1.7,18.2	1.93	0.179	CC*CH*ST	1.6,17.8	1.97	0.175
TA*CC*CH*ST	2.6,28.4	0.32	0.783	TA*CC*CH*ST	2.7,29.8	0.24	0.851

* indicates statistical significance at the 0.05 level or better

Table 5.9. ANOVA summary table for analysis of the amplitude of the 500-900 ms region elicited by frequent, target and rare non-target stimuli for the two tasks, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	4.44	0.059
Condition (CC)	1.9,21.1	1.13	0.340
Chain (CH)	1.5,16.8	4.41	0.038*
Site (ST)	1.2,12.9	26.46	0.000*
TA*CC	1.4,15.3	3.08	0.089
TA*CH	1.8,20.3	0.90	0.411
TA*ST	1.1,12.3	0.08	0.805
CC*CH	2.7,29.7	0.48	0.676
CC*ST	2.1,23.0	15.59	0.000*
CH*ST	3.3,36.1	12.09	0.000*
TA*CC*CH	3.2,35.4	3.36	0.027*
TA*CC*ST	2.3,25.0	0.17	0.872
TA*CH*ST	2.8,30.3	1.15	0.344
CC*CH*ST	3.6,39.1	3.51	0.019*
TA*CC*CH*ST	3.7,41.2	1.93	0.128

RESCALED AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,11	0.05	0.825
Condition (CC)	1.6,17.5	0.09	0.871
Chain (CH)	1.5,16.2	6.16	0.016*
Site (ST)	1.2,13.1	18.16	0.001*
TA*CC	1.6,18.1	0.17	0.800
TA*CH	1.9,21.1	0.32	0.717
TA*ST	1.2,13.2	0.02	0.931
CC*CH	2.3,24.9	1.02	0.385
CC*ST	1.6,17.3	0.45	0.599
CH*ST	3.0,32.6	12.03	0.000*
TA*CC*CH	2.4,26.7	1.58	0.223
TA*CC*ST	2.7,29.2	0.16	0.902
TA*CH*ST	2.6,28.8	0.62	0.583
CC*CH*ST	3.8,41.4	0.92	0.454
TA*CC*CH*ST	2.5,27.5	1.56	0.225

* indicates statistical significance at the 0.05 level or better

Table 6.2. ANOVA summary table for analysis of the amplitude of the N100 elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1.3,14.8	2.92	0.100	Condition (CC)	1.7,18.7	2.41	0.123
Chain (CH)	1.3,14.2	19.66	0.000*	Chain (CH)	1.3,14.5	21.25	0.000*
Site (ST)	1.2,12.7	16.56	0.001*	Site (ST)	1.1,12.3	18.48	0.001*
CC*CH	2.0,22.4	1.57	0.231	CC*CH	2.2,24.7	0.41	0.691
CC*ST	2.0,21.6	6.74	0.006*	CC*ST	2.1,22.9	10.33	0.001*
CH*ST	2.4,26.2	2.73	0.076	CH*ST	2.4,26.9	2.65	0.080
CC*CH*ST	2.5,27.9	3.56	0.033	CC*CH*ST	3.3,36.1	3.41	0.025*

* indicates statistical significance at the 0.05 level or better

Table 6.3. ANOVA summary table for analysis of the amplitude of the P170 elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1.1,12.2	4.95	0.043*	Condition (CC)	1.1,11.9	0.01	0.925
Chain (CH)	1.3,14.2	5.01	0.035*	Chain (CH)	1.3,14.2	5.50	0.027*
Site (ST)	1.4,15.2	6.96	0.012*	Site (ST)	1.4,15.0	7.11	0.012*
CC*CH	1.8,19.7	0.23	0.769	CC*CH	1.8,19.3	0.35	0.680
CC*ST	1.9,20.6	1.92	0.174	CC*ST	2.0,21.8	1.86	0.180
CH*ST	3.1,34.0	12.33	0.000*	CH*ST	3.0,33.5	12.33	0.000*
CC*CH*ST	3.2,35.1	2.56	0.067	CC*CH*ST	3.2,35.6	2.51	0.071

* indicates statistical significance at the 0.05 level or better

Table 6.4. ANOVA summary table for analysis of the amplitude of the 400-700 ms region elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1.1,12.6	0.12	0.768	Condition (CC)	1.3,13.9	0.12	0.788
Chain (CH)	1.7,18.7	2.52	0.114	Chain (CH)	1.8,20.3	4.90	0.020*
Site (ST)	1.1,11.8	23.06	0.000*	Site (ST)	1.0,11.3	11.60	0.005*
CC*CH	1.8,20.3	0.12	0.876	CC*CH	1.8,20.0	1.25	0.306
CC*ST	1.7,18.8	21.11	0.000*	CC*ST	1.9,20.5	0.71	0.494
CH*ST	2.2,24.5	6.81	0.003*	CH*ST	2.1,23.1	4.42	0.022*
CC*CH*ST	2.8,31.2	5.41	0.005*	CC*CH*ST	3.2,35.7	0.88	0.463

* indicates statistical significance at the 0.05 level or better

Table 6.6. ANOVA summary table for analysis of the amplitude of the 350-550 ms region elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	0.09	0.767	Condition (CC)	1,11	0.01	0.941
Chain (CH)	1.8,19.9	4.19	0.034*	Chain (CH)	1.7,19.2	4.61	0.027*
Site (ST)	1.0,11.3	14.47	0.003*	Site (ST)	1.0,11.5	10.47	0.007*
CC*CH	1.7,18.7	0.88	0.415	CC*CH	1.4,14.9	1.64	0.226
CC*ST	1.2,13.2	27.62	0.000*	CC*ST	1.3,14.3	1.95	0.185
CH*ST	1.9,20.4	2.91	0.081	CH*ST	2.0,22.4	3.01	0.069
CC*CH*ST	3.2,35.6	0.64	0.606	CC*CH*ST	2.4,25.9	1.66	0.207

* indicates statistical significance at the 0.05 level or better

Table 7.2. ANOVA summary table for analysis of the amplitude of the N100 elicited by target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	0.25	0.627	Condition (CC)	1,11	0.15	0.710
Chain (CH)	1.3,13.9	26.12	0.000*	Chain (CH)	1.3,14.0	26.29	0.000*
Site (ST)	1.3,14.0	13.44	0.002*	Site (ST)	1.3,13.9	13.33	0.002*
CC*CH	1.8,20.2	0.64	0.525	CC*CH	1.8,19.8	0.80	0.450
CC*ST	1.4,15.9	0.03	0.941	CC*ST	1.4,15.7	0.04	0.912
CH*ST	2.5,27.0	1.40	0.267	CH*ST	2.5,27.1	1.41	0.264
CC*CH*ST	3.1,34.5	1.41	0.256	CC*CH*ST	3.1,34.2	1.47	0.240

* indicates statistical significance at the 0.05 level or better

Table 7.3. ANOVA summary table for analysis of the amplitude of the P170 elicited by target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	46.70	0.000*	Condition (CC)	1,11	1.41	0.260
Chain (CH)	1.4,15.2	3.21	0.084	Chain (CH)	1.4,15.1	3.33	0.078
Site (ST)	1.1,12.1	1.39	0.267	Site (ST)	1.1,12.1	1.33	0.277
CC*CH	1.8,20.2	5.58	0.013*	CC*CH	1.8,19.7	5.75	0.013*
CC*ST	1.5,16.7	12.11	0.001*	CC*ST	1.5,16.6	10.38	0.002*
CH*ST	2.5,28.0	14.91	0.000*	CH*ST	2.5,28.0	14.45	0.000*
CC*CH*ST	2.9,32.0	1.23	0.317	CC*CH*ST	2.8,31.3	1.31	0.291

* indicates statistical significance at the 0.05 level or better

Table 7.5. ANOVA summary table for analysis of the amplitude of the N200 elicited by target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	0.09	0.772	Condition (CC)	1,11	0.19	0.671
Chain (CH)	1.6,18.1	3.71	0.052	Chain (CH)	1.7,19.2	3.46	0.058
Site (ST)	1.6,18.0	11.70	0.001*	Site (ST)	1.6,17.7	11.29	0.001*
CC*CH	1.5,16.3	1.68	0.219	CC*CH	1.8,20.1	0.62	0.530
CC*ST	1.6,17.7	6.08	0.013*	CC*ST	1.3,14.1	1.30	0.288
CH*ST	2.3,25.8	0.40	0.702	CH*ST	2.4,25.9	0.39	0.711
CC*CH*ST	2.2,24.6	3.00	0.064	CC*CH*ST	2.4,26.6	3.61	0.034*

* indicates statistical significance at the 0.05 level or better

Table 7.6. ANOVA summary table for analysis of the amplitude of the 500-900 ms region elicited by target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1,11	3.32	0.096	Condition (CC)	1,11	0.06	0.810
Chain (CH)	1.4,15.1	3.84	0.058	Chain (CH)	1.4,15.3	3.64	0.064
Site (ST)	1.1,11.9	49.54	0.000*	Site (ST)	1.1,12.0	46.28	0.000*
CC*CH	1.8,19.8	1.84	0.188	CC*CH	1.6,18.1	0.35	0.669
CC*ST	1.2,12.7	0.83	0.394	CC*ST	1.2,12.8	0.29	0.631
CH*ST	1.7,18.4	6.78	0.009*	CH*ST	1.6,18.1	6.36	0.011*
CC*CH*ST	2.6,28.4	4.55	0.013*	CC*CH*ST	2.6,28.7	2.33	0.103

* indicates statistical significance at the 0.05 level or better

Table 7.12. ANOVA summary table for analysis of the amplitude of the N100 elicited by target and rare non-target stimuli in 'frequents present' task and 'omitted frequents' task, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Task (TA)	1,17	14.70	0.001*	Task (TA)	1,17	1.94	0.182
Condition (CC)	1,17	1.28	0.275	Condition (CC)	1,17	0.08	0.786
Chain (CH)	1.6,28.0	46.84	0.000*	Chain (CH)	1.7,28.6	46.70	0.000*
Site (ST)	1.6,28.0	19.39	0.000*	Site (ST)	1.6,27.6	21.04	0.000*
TA*CC	1,17	0.56	0.464	TA*CC	1,17	0.21	0.653
TA*CH	1.7,29.0	9.37	0.001*	TA*CH	2.0,33.8	0.32	0.726
TA*ST	1.7,29.2	10.03	0.001*	TA*ST	1.8,31.2	13.20	0.000*
CC*CH	2.0,33.4	0.01	0.986	CC*CH	1.9,31.6	0.56	0.562
CC*ST	1.4,23.4	8.53	0.004*	CC*ST	1.5,26.0	8.32	0.003*
CH*ST	2.6,44.9	14.44	0.000*	CH*ST	2.7,45.2	13.43	0.000*
TA*CC*CH	1.7,29.2	0.74	0.463	TA*CC*CH	1.5,26.0	0.65	0.488
TA*CC*ST	1.3,22.0	2.22	0.146	TA*CC*ST	1.5,25.1	0.58	0.517
TA*CH*ST	2.3,39.3	9.53	0.000*	TA*CH*ST	2.4,40.8	4.47	0.013*
CC*CH*ST	3.2,54.3	1.54	0.214	CC*CH*ST	3.0,51.8	0.94	0.430
TA*CC*CH*ST	3.1,53.1	0.73	0.541	CC*CH*ST	3.0,51.3	0.49	0.690

* indicates statistical significance at the 0.05 level or better

Table 7.13. ANOVA summary table for analysis of the amplitude of the P170 elicited by target and rare non-target stimuli in 'frequents present' task and 'omitted frequents' task, before and after rescaling.

RAW AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,17	16.92	0.001*
Condition (CC)	1,17	0.00	1.000
Chain (CH)	1.4,24.4	4.07	0.042*
Site (ST)	1.3,22.6	0.66	0.463
TA*CC	1,17	1.76	0.202
TA*CH	1.5,24.8	1.48	0.245
TA*ST	1.9,31.6	1.64	0.213
CC*CH	1.7,28.7	10.56	0.001*
CC*ST	1.2,20.8	8.35	0.006*
CH*ST	2.4,40.5	13.37	0.000*
TA*CC*CH	1.7,28.2	8.86	0.002*
TA*CC*ST	1.2,20.5	1.81	0.195
TA*CH*ST	2.5,43.1	7.50	0.001*
CC*CH*ST	3.5,59.3	4.40	0.005*
TA*CC*CH*ST	2.6,44.2	2.54	0.077

RESCALED AMPLITUDE			
Factors	df	F	Prob
Task (TA)	1,17	0.00	0.983
Condition (CC)	1,17	0.47	0.501
Chain (CH)	1.4,24.4	3.50	0.060
Site (ST)	1.3,22.0	0.63	0.472
TA*CC	1,17	0.01	0.916
TA*CH	1.5,25.2	0.85	0.407
TA*ST	1.9,32.4	1.30	0.286
CC*CH	1.8,29.8	11.93	0.000*
CC*ST	1.2,19.7	7.79	0.009*
CH*ST	2.5,43.1	12.77	0.000*
TA*CC*CH	1.8,30.7	9.47	0.001*
TA*CC*ST	1.2,20.9	3.87	0.055
TA*CH*ST	2.9,48.8	3.90	0.015*
CC*CH*ST	3.4,58.3	4.60	0.004*
CC*CH*ST	3.0,50.5	2.42	0.077

* indicates statistical significance at the 0.05 level or better

Table 7.14. ANOVA summary table for analysis of the amplitude of the 500-900 ms region elicited by target and rare non-target stimuli in 'frequents present' task and 'omitted frequents' task, before and after rescaling.

RAW AMPLITUDE

Factors	df	F	Prob
Task (TA)	1,17	15.23	0.001*
Condition (CC)	1,17	1.92	0.185
Chain (CH)	1.9,32.7	7.23	0.003*
Site (ST)	1.1,19.2	60.75	0.000*
TA*CC	1,17	1.67	0.215
TA*CH	1.9,31.6	7.54	0.003*
TA*ST	1.2,20.3	6.25	0.017*
CC*CH	1.9,32.5	6.01	0.007*
CC*ST	1.1,19.5	3.21	0.084
CH*ST	3.3,55.7	7.07	0.000*
TA*CC*CH	2.0,34.0	1.48	0.243
TA*CC*ST	1.3,21.7	2.19	0.150
TA*CH*ST	2.5,42.5	2.66	0.070
CC*CH*ST	3.1,52.0	5.15	0.003*
TA*CC*CH*ST	3.1,53.1	1.45	0.239

0.94

* indicates statistical significance at the 0.05 level or better0.49

RESCALED AMPLITUDE

Factors	df	F	Prob
Task (TA)	1,17	0.10	0.758
Condition (CC)	1,17	0.10	0.755
Chain (CH)	1.9,33.0	5.89	0.007*
Site (ST)	1.1,19.1	64.20	0.000*
TA*CC	1,17	0.25	0.622
TA*CH	1.9,32.3	7.81	0.002*
TA*ST	1.2,20.1	4.13	0.050*
CC*CH	1.9,32.2	4.43	0.022*
CC*ST	1.2,19.8	0.70	0.431
CH*ST	3.2,54.4	5.78	0.001*
TA*CC*CH	2.0,33.9	0.70	0.501
TA*CC*ST	1.3,21.4	0.58	0.491
TA*CH*ST	2.7,45.4	2.36	0.091
CC*CH*ST	3.0,51.3	3.09	0.035*
CC*CH*ST	3.0,51.5	1.09	0.364

Table 8.4. ANOVA summary table for analysis of the amplitude of the N100 elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1.6,17.1	10.54	0.002*	Condition (CC)	1.4,15.0	0.47	0.559
Chain (CH)	1.4,15.0	45.41	0.000*	Chain (CH)	1.3,14.7	43.90	0.000*
Site (ST)	1.2,13.7	15.53	0.001*	Site (ST)	1.2,13.6	14.84	0.001*
CC*CH	2.6,28.3	2.58	0.081	CC*CH	2.3,25.7	0.72	0.518
CC*ST	1.7,18.6	6.20	0.011*	CC*ST	1.6,17.7	4.24	0.039*
CH*ST	3.2,34.7	9.54	0.000*	CH*ST	3.2,34.7	9.41	0.000*
CC*CH*ST	3.7,40.8	0.75	0.556	CC*CH*ST	3.8,42.3	0.70	0.590

* indicates statistical significance at the 0.05 level or better

Table 8.5. ANOVA summary table for analysis of the amplitude of the P170 elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1.5,16.8	5.46	0.021*	Condition (CC)	1.8,20.0	0.02	0.968
Chain (CH)	1.3,14.8	19.24	0.000*	Chain (CH)	1.3,14.5	15.17	0.001*
Site (ST)	1.5,16.6	5.42	0.022*	Site (ST)	1.5,16.6	4.10	0.046*
CC*CH	2.3,25.6	3.79	0.031*	CC*CH	2.1,22.8	1.68	0.209
CC*ST	2.2,23.7	16.46	0.000*	CC*ST	2.3,25.6	7.80	0.002*
CH*ST	2.7,30.0	13.26	0.000*	CH*ST	2.7,29.8	11.87	0.000*
CC*CH*ST	4.2,46.1	1.06	0.389	CC*CH*ST	4.4,48.6	2.08	0.092

* indicates statistical significance at the 0.05 level or better

Table 8.6. ANOVA summary table for analysis of the amplitude of the 500-900 ms region elicited by frequent, target and rare non-target stimuli, before and after rescaling.

RAW AMPLITUDE				RESCALED AMPLITUDE			
Factors	df	F	Prob	Factors	df	F	Prob
Condition (CC)	1.6,17.4	1.44	0.261	Condition (CC)	1.9,20.5	0.15	0.845
Chain (CH)	1.8,20.1	4.70	0.024*	Chain (CH)	1.8,19.8	3.10	0.072
Site (ST)	1.7,18.7	25.34	0.000*	Site (ST)	1.5,16.3	12.76	0.001*
CC*CH	2.3,25.2	5.10	0.011*	CC*CH	2.3,25.4	1.25	0.308
CC*ST	1.9,21.4	11.98	0.000*	CC*ST	1.9,20.6	0.46	0.624
CH*ST	2.8,30.5	4.09	0.017*	CH*ST	3.2,35.0	4.00	0.014*
CC*CH*ST	3.5,38.8	1.35	0.273	CC*CH*ST	3.0,33.0	0.91	0.445

* indicates statistical significance at the 0.05 level or better

Table 9.2. ANOVA summary table for analysis of the amplitude of the N100 elicited by target and rare non-target stimuli in each block of 200 trials, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.3,25.5	1.29	0.297
Condition (CC)	1,11	0.11	0.746
Chain (CH)	1.6,17.4	18.92	0.000*
Site (ST)	1.2,12.8	14.94	0.001*
BL*CC	2.6,28.7	2.89	0.060
BL*CH	3.6,39.4	0.98	0.423
BL*ST	3.5,38.9	1.4	0.256
CC*CH	1.7,18.5	0.43	0.619
CC*ST	1.2,13.3	31.68	0.000*
CH*ST	2.3,25.3	2.43	0.102
BL*CC*CH	2.7,29.7	0.67	0.562
BL*CC*ST	3.0,33.1	0.95	0.428
BL*CH*ST	5.4,59.7	0.92	0.479
CC*CH*ST	2.5,27.0	1.05	0.377
BL*CC*CH*ST	4.9,54.0	0.81	0.548

RESCALED AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.2,24.3	0.10	0.924
Condition (CC)	1,11	2.93	0.116
Chain (CH)	1.6,17.1	19.02	0.000*
Site (ST)	1.2,12.8	14.88	0.001*
BL*CC	2.4,26.5	0.00	0.999
BL*CH	3.7,40.3	0.52	0.704
BL*ST	3.3,36.5	0.60	0.632
CC*CH	1.7,18.4	0.69	0.488
CC*ST	1.2,13.4	30.41	0.000*
CH*ST	2.3,25.4	2.46	0.099
BL*CC*CH	2.8,30.6	1.06	0.377
BL*CC*ST	3.0,32.7	0.62	0.605
BL*CH*ST	5.3,58.2	1.11	0.367
CC*CH*ST	2.5,27.0	0.96	0.410
BL*CC*CH*ST	4.9,53.4	0.82	0.540

Table 9.3. ANOVA summary table for analysis of the amplitude of the P170 elicited by target and rare non-target stimuli in each block of 200 trials, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.3,25.8	0.27	0.799
Condition (CC)	1,11	22.25	0.001*
Chain (CH)	1.7,18.9	21.40	0.000*
Site (ST)	1.4,15.1	2.65	0.117
BL*CC	2.6,28.3	1.69	0.197
BL*CH	3.9,43.1	1.15	0.348
BL*ST	2.6,29.8	0.34	0.772
CC*CH	2.0,21.6	1.70	0.207
CC*ST	1.5,16.6	11.37	0.002*
CH*ST	2.3,25.5	7.27	0.002*
BL*CC*CH	3.2,35.2	0.62	0.616
BL*CC*ST	3.6,39.8	0.84	0.496
BL*CH*ST	5.5,60.1	1.53	0.191
CC*CH*ST	2.8,30.9	2.29	0.102
BL*CC*CH*ST	4.9,53.6	1.61	0.176

RESCALED AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.3,25.3	0.13	0.904
Condition (CC)	1,11	0.16	0.699
Chain (CH)	1.8,19.7	22.21	0.000*
Site (ST)	1.5,16.0	6.01	0.017*
BL*CC	1.9,20.8	0.07	0.925
BL*CH	2.8,31.2	0.39	0.748
BL*ST	2.7,30.1	0.69	0.549
CC*CH	1.9,20.5	0.27	0.750
CC*ST	1.3,14.3	0.05	0.884
CH*ST	2.3,25.6	8.65	0.001*
BL*CC*CH	3.8,41.4	0.59	0.658
BL*CC*ST	3.4,37.9	0.18	0.931
BL*CH*ST	4.2,46.7	1.19	0.330
CC*CH*ST	2.6,28.4	1.50	0.239
BL*CC*CH*ST	4.1,44.6	1.11	0.366

Table 9.4. ANOVA summary table for analysis of the amplitude of the 500-900 ms region elicited by target and rare non-target stimuli in each block of 200 trials, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.4,26.1	1.44	0.255
Condition (CC)	1,11	13.50	0.004*
Chain (CH)	1.7,18.7	6.57	0.009*
Site (ST)	1.2,12.9	39.58	0.000*
BL*CC	2.1,23.3	1.46	0.254
BL*CH	3.9,42.8	0.68	0.607
BL*ST	2.8,30.9	5.17	0.006*
CC*CH	1.8,19.5	6.44	0.009*
CC*ST	1.3,13.8	2.63	0.123
CH*ST	2.7,29.8	11.28	0.000*
BL*CC*CH	3.9,42.7	0.71	0.581
BL*CC*ST	3.2,34.9	4.92	0.005*
BL*CH*ST	5.0,54.6	0.77	0.576
CC*CH*ST	3.1,33.6	4.00	0.015*
BL*CC*CH*ST	5.2,57.4	1.36	0.251

RESCALED AMPLITUDE			
Factors	df	F	Prob
Block (BL)	2.0,21.8	0.04	0.964
Condition (CC)	1,11	0.55	0.472
Chain (CH)	1.7,19.2	5.36	0.017*
Site (ST)	1.2,12.8	39.83	0.000*
BL*CC	1.9,20.9	0.40	0.666
BL*CH	3.6,39.9	0.51	0.711
BL*ST	3.1,33.6	0.23	0.881
CC*CH	1.8,19.7	2.56	0.108
CC*ST	1.3,13.9	0.55	0.510
CH*ST	2.8,30.5	10.71	0.000*
BL*CC*CH	3.4,37.3	0.53	0.687
BL*CC*ST	3.1,34.2	0.08	0.974
BL*CH*ST	4.5,50.0	0.83	0.527
CC*CH*ST	3.0,32.9	1.73	0.180
BL*CC*CH*ST	5.5,60.2	1.84	0.114

Table 10.2. ANOVA summary table for analysis of the amplitude of the N100 elicited by target and rare non-target stimuli for each of the three experimental conditions, before and after rescaling

RAW AMPLITUDE

Factors	df	F	Prob
Stimulus (S)	1,15	2.52	0.134
Condition (CC)	1.5,23.1	0.96	0.373
Chain (CH)	1.7,25.0	26.73	0.000*
Site (ST)	1.2,17.6	21.57	0.000*
S*CC	1.9,28.0	0.76	0.468
S*CH	1.7,25.2	0.99	0.370
S*ST	1.1,16.8	1.42	0.255
CC*CH	3.3,49.1	0.66	0.594
CC*ST	2.2,32.4	2.45	0.099
CH*ST	3.3,49.8	4.09	0.009*
S*CC*CH	2.9,43.3	2.09	0.119
S*CC*ST	2.2,33.0	0.44	0.666
S*CH*ST	3.3,49.3	0.84	0.486
CC*CH*ST	5.0,75.7	1.61	0.167
S*CC*CH*ST	3.4,50.5	1.43	0.245

RESCALED AMPLITUDE

Factors	df	F	Prob
Stimulus (S)	1,15	0.21	0.651
Condition (CC)	1.5,22.1	0.53	0.539
Chain (CH)	1.6,24.6	25.37	0.000*
Site (ST)	1.2,17.7	20.41	0.000*
S*CC	1.7,26.2	0.00	0.996
S*CH	1.8,26.5	0.38	0.659
S*ST	1.1,17.2	0.95	0.354
CC*CH	3.2,47.4	1.53	0.218
CC*ST	2.1,31.2	1.38	0.269
CH*ST	3.3,49.0	3.85	0.013*
S*CC*CH	2.7,41.1	1.87	0.154
S*CC*ST	2.1,31.5	0.23	0.807
S*CH*ST	3.3,48.8	0.92	0.445
CC*CH*ST	5.1,76.7	1.36	0.247
S*CC*CH*ST	3.5,52.3	1.55	0.207

* indicates statistical significance at the 0.05 level or better

Table 10.3. ANOVA summary table for analysis of the amplitude of the P170 elicited by target and rare non-target stimuli for each of the three experimental conditions, before and after rescaling

RAW AMPLITUDE			
Factors	df	F	Prob
Stimulus (S)	1,15	1.70	0.212
Condition (CC)	1.5,21.8	1.53	0.238
Chain (CH)	1.9,28.6	15.88	0.000*
Site (ST)	1.5,21.8	6.63	0.010*
S*CC	1.9,27.9	0.33	0.704
S*CH	2.0,29.8	0.28	0.760
S*ST	1.1,16.7	3.10	0.094
CC*CH	2.2,32.3	1.28	0.293
CC*ST	2.2,32.6	3.28	0.047*
CH*ST	2.9,44.1	11.22	0.000*
S*CC*CH	2.9,43.4	0.48	0.688
S*CC*ST	1.9,28.8	0.66	0.517
S*CH*ST	3.2,48.3	2.27	0.088
CC*CH*ST	4.7,70.9	1.44	0.224
S*CC*CH*ST	4.3,64.1	3.96	0.005*

RESCALED AMPLITUDE			
Factors	df	F	Prob
Stimulus (S)	1,15	0.23	0.640
Condition (CC)	1.7,25.8	0.04	0.947
Chain (CH)	1.9,29.2	14.14	0.000*
Site (ST)	1.4,21.0	5.26	0.023*
S*CC	1.8,26.3	0.23	0.770
S*CH	1.8,27.4	0.17	0.822
S*ST	1.1,17.1	2.25	0.150
CC*CH	2.7,39.8	0.81	0.481
CC*ST	1.9,28.0	1.47	0.248
CH*ST	2.9,43.2	10.46	0.000*
S*CC*CH	2.9,43.2	0.25	0.854
S*CC*ST	1.6,24.7	0.49	0.582
S*CH*ST	3.4,51.1	4.25	0.007*
CC*CH*ST	4.7,70.3	2.15	0.074
S*CC*CH*ST	4.4,65.5	2.81	0.029*

* indicates statistical significance at the 0.05 level or better

Table 10.4. ANOVA summary table for analysis of the amplitude of the 400-800 ms region elicited by target stimuli for each of the three experimental conditions before rescaling at all electrode sites

RAW AMPLITUDE

Factors	df	F	Prob
Condition (CC)	1.8,27.1	1.11	0.339
Chain (CH)	1.8,27.2	5.61	0.011*
Site (ST)	1.3,20.1	64.81	0.000*
CC*CH	3.2,47.8	8.66	0.000*
CC*ST	2.0,29.7	7.82	0.002*
CH*ST	2.8,41.8	16.30	0.000*
CC*CH*ST	5.4,81.7	0.50	0.790

* indicates statistical significance at the 0.05 level or better

Table 10.5. ANOVA summary tables for analysis of the amplitude of the 400-800 ms region elicited by target stimuli for each of the three experimental conditions, at frontal and parietal sites before rescaling

FRONTAL SITES

Factors	df	F	Prob
Condition (CC)	1.8,27.0	2.68	0.092
Chain (CH)	1.9,28.0	10.96	0.000*
CC*CH	3.1,47.2	4.91	0.004*

PARIETAL SITES

Factors	df	F	Prob
Condition (CC)	1.5,22.5	6.97	0.008*
Chain (CH)	1.7,25.3	15.85	0.000*
CC*CH	2.7.39.9	4.59	0.010*

* indicates statistical significance at the 0.05 level or better

Table 10.6. ANOVA summary table for analysis of the amplitude of the 400-800 ms region elicited by rare non-target novel sounds for each of the three experimental conditions before rescaling at all electrode sites

RAW AMPLITUDE

Factors	df	F	Prob
Condition (CC)	1.8,27.1	2.05	0.152
Chain (CH)	1.5,22.6	2.89	0.089
Site (ST)	1.4,20.8	69.17	0.000*
CC*CH	3.0,44.3	2.54	0.069
CC*ST	1.9,28.8	1.15	0.332
CH*ST	2.5,37.5	7.57	0.001*
CC*CH*ST	4.1,61.8	1.20	0.319

* indicates statistical significance at the 0.05 level or better

Table 10.7. ANOVA summary tables for analysis of the amplitude of the 400-800 ms region elicited by rare non-target novel sounds for each of the three experimental conditions, at frontal and parietal sites before rescaling

FRONTAL SITES

Factors	df	F	Prob
Condition (CC)	1.9,29.2	0.38	0.682
Chain (CH)	1.4,21.5	4.88	0.027*
CC*CH	3.2,48.3	1.19	0.326

PARIETAL SITES

Factors	df	F	Prob
Condition (CC)	1.6,24.1	4.12	0.037*
Chain (CH)	1.6,23.6	6.83	0.007*
CC*CH	3.0,44.8	2.56	0.067

* indicates statistical significance at the 0.05 level or better

ABBREVIATIONS USED THROUGHOUT THIS THESIS

EEG: electroencephalogram

ERP: event-related potential

MEG: magnetoencephalogram

MMN: mismatch negativity

PN: processing negativity

OR: orienting response

RT: reaction time

SD: standard deviation